ERRATUM

Page 354, third line from end of second paragraph:
for 'areas) or are mane-fleas. The archurieopsyllines include . . . '
read 'areas) or are murine-fleas. The archaeopsyllines include . . . '.

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[EV]OLUTION AND TAXONOMY OF FLEAS (SIPHONAPTERA), BASED ON COLLECTIONS FROM GUNONG BENOM AND ELSEWHERE IN SOUTH-EAST ASIA.

II. CONVERGENT EVOLUTION

By ROBERT TRAUB

CONTENTS

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12. NOTES ON ZOOGEOGRAPHY, CONVERGENT EVOLUTION AND TAXONOMY OF FLEAS (SIPHONAPTERA), BASED ON COLLECTIONS FROM GUNONG BENOM AND ELSEWHERE IN SOUTH-EAST ASIA.

II. CONVERGENT EVOLUTION

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ABSTRACT

In the Order Siphonaptera there are many examples of the moulding effect of the environment —be it the fur or feathers of the host or its habitat—upon the physiognomy of the flea, resulting in a uniformity of appearance that may reflect convergent evolution, and not phylogeny or even homology.

Additional data are presented suggesting that the pattern and shape of the spines of the pronotal comb of fleas may be more frequently adaptive than had been generally supposed, as indicated by the fact that unrelated fleas often have the same type of comb (or vestiture in general), while, in contrast, a variety of patterns may be exhibited by a single genus of flea, depending upon the host. Thus, in the squirrel-fleas in general, the second or third spines of the comb (counting from the bottom) tend to be relatively broad, and often slightly overlapping near the base. This has been noted in 13 genera and 3 families of fleas, and in all instances these spines are proportionately broader and shorter than in the case of members of the same taxon which are "fur-fleas" of murids, cricetines, insectivores, etc. The trend is particularly well developed in fleas of diurnal tree-squirrels and has occurred on all four continents where these rodents occur. It is believed that modifications of this sort are directly associated with the diameter and shape of the hairs of the host, and it seems likely that the overlapping second and third spines of the comb of fleas of tree-squirrels would grasp the hairs in a scissors-like grip if the flea were pulled backwards by the host in attempts at dislodgement. Precise data on this point are lacking insofar as concerns fleas of squirrels.

The modifications of the pronotal comb are by no means always correlated with the vestiture of the host, as is indicated by the fact that, regardless of host, 17 genera of fleas, representing 3 families and 5 subfamilies, exhibit the same unusual type of ctenidium, in which the spines are exceptionally or notably short and broad and relatively few in number. These are all "nest-fleas" in that they are much more prevalent in the nest than on the host, etc. and show reduction in general chaetotaxy, modifications of the thorax and other specialized features. The type of comb in these fleas is accordingly believed to represent a general trend towards reduction which is a feature in the evolutionary development of the nest-habit, which is discussed in detail.

Fleas of volant and gliding hosts such as bats, birds and flying-squirrels have solved the dilemma of finding such a bird or mammal without a disastrous fall in the process and yet managing to remain affixed to the host despite its active flight or aerial gymnastics. One common way this has been accomplished is by becoming crawlers, rather than jumpers, and developing supernumerary spines in the pronotal comb, and/or additional combs, long bristles, etc. or by anchoring mouthparts. Such fleas often possess a thorax in which the pleural arch, under which is housed the elastic resilin which provides the power for leaping, has become completely or partially reduced. This thoracic modification is also seen in "nest-fleas" inhabiting tall trees, banks and caves, etc., where a fall would be hazardous, even if survived, because of the small chance of finding a suitable host. It likewise occurs in many nest-fleas of terrestrial or underground nests, and in other habitats, and reasons are advanced to indicate that the condition

(in all cases) is adaptive. This modification of the thorax has been achieved by a variety of morphological changes, emphasizing that these are examples of convergent evolution.

The relative degree of the development of the eye in fleas is also associated with the habits of the flea, or its host or environment. In many instances, reduction of the eye accompanies that of the metathorax and loss of the pleural arch, but notable exceptions are pointed out. The behaviour of various kinds of fleas in finding and feeding on their hosts is discussed.

I. INTRODUCTION

FLEAS are highly modified morphologically for an ectoparasitic existence (Rothschild, 1917; Ioff, 1929; Traub, 1966; Traub & Evans, 1967), and the specializations exhibited include patterns of ctenidia (combs of spines) and chaetotaxy that somehow reflect the environment provided by the host (Traub & Barrera, 1966; Humphries, 1966, 1967; Traub, 1968, 1969), rather than merely the phylogeny or taxonomic position of the flea. The modifications in some instances are obviously adaptive and are concerned with the flea maintaining a grip on the host and escaping capture. Others are difficult or impossible to explain by referring to the vestiture of the infested mammal or bird, but can be correlated with the haunts or habits of the host. Some of the fleas discussed in the first article in this series (Traub, 1972a) illustrate such examples of Convergent Evolution, and these and other relevant taxa will be treated in the present paper and new points will be presented along such lines.

That the nature of the pronotal comb is adaptive is indicated by two generalizations: (1) The same pattern of comb is frequently exhibited by unrelated fleas parasitizing the same host, and (2) Within a genus there may be a variety of types of combs, depending upon the host. Therefore, by way of background, variations of the type of pronotal comb seen in a single taxon will be mentioned and associated with certain kinds of hosts. The characteristic features of the class of pronotal comb will be noted, and tabled data and illustrations will be presented for various genera of fleas, and for various kinds of fleas, such as squirrel-fleas, murid-fleas, nest-fleas, etc. In the section on discussion, it is pointed out that while in many instances the precise configuration of the comb can be explained by the nature of the hairs of the host, this does not apply to the type of comb seen in fleas which are characteristic inhabitants of underground nests, and which are modified accordingly, even though a variety of taxa, often unrelated, are represented. In order to demonstrate that this is so, and to offer an explanation, the phenomenon of nest-fleas is discussed in some detail and this leads to a consideration and review of two features commonly seen in nest-fleas, viz., the marked reduction of the eye and loss of the pleural arch. It is pointed out that in some nest-fleas, however, the eye is unusually large and this is shown to be adaptive, as is the loss of the pleural arch in bat-fleas, which are not nest-fleas. Thus, the morphological modifications are shown to be connected with the pattern of life of the flea, and often with the habits of the host.

It should be noted that no attempt is made in this article to review all of the various modifications in the pattern of pronotal combs seen in Siphonaptera. For example, the remarkable and well-known convergence exhibited by combed bird-fleas, in which the pronotal comb always bears a significantly greater number of spines than do allied forms infesting mammals, and which are otherwise specialized, will be treated in detail in a subsequent article. This phenomenon has now been

noted in nine genera, representing three families (including a new genus and new records known to the writer). The type of comb deemed characteristic of fleas infesting nocturnal arboreal hosts has been mentioned previously (Traub, 1969), while Traub & Evans (1967) referred to some ctenidia of insectivore-fleas and desert-fleas, etc. and Traub & Barrera (1966) discussed ctenidia in shrew-fleas. Other points about ctenidia were treated by Traub in 1968, and some important considerations remain for future treatment. Instead, the present paper will primarily deal with the pronotal comb of fleas infesting arboreal squirrels and with that of nest-fleas in general, with passing reference to murid-fleas, etc., while, the resulting discussion leads to the points mentioned above.

II. BACKGROUND

The pronotal comb of *Medwayella* Traub, 1972 (fig. 6),[1] a genus which generally infests arboreal and semi-arboreal sciurids, resembles that seen in genera of fleas which are characteristic parasites of tree-squirrels (figs 1–14). However, before considering that subject further, it is instructive to review the features of the pronotal comb in some other fleas, particularly *Lentistivalius* Traub, 1972, in which the 5 known species are closely allied, as indicated in the article on *Medwayella*, but which vary considerably in the kind of host infested and their geographical location. In this group of fleas it has been possible to glance at the spines of the comb and correctly state whether the host is a bird, rodent or shrew. Although no bird-fleas had been known in the family Pygiopsyllidae prior to 1950, the author of *L. insolli* (Traub, 1950b) suggested that the species infested birds because the pronotal comb (vide fig. 18) consisted of 26–28 narrow, fairly straight, closely set spines and the comb did not extend far enough ventrad to cover the third vinculum, thereby paralleling the condition in bird-fleas of the families Ceratophyllidae and Leptopsyllidae. (This belief about the avian hosts of *L. insolli* turned out to be correct.) In each instance, the mammal-infesting fleas related to all of these bird-fleas bear combs of 18–24 spines (generally around 20), while the spines are broader, differently shaped, i.e. concave or pointed, or else, if there is a larger number of spines present, the comb extends further ventrad, over the vinculum (Traub, 1969). On the other hand, when Smit (1958) described the flea now called *L. alienus*, he pointed out that the appearance of the comb (vide fig. 16) led him to state that the host was a rodent, because the spines were "fairly straight," unlike *L. ferinus* (Rothschild, 1908) which is a shrew-flea, where "the spines are blunt, distinctly curved and longer than the pronotum," as shown in fig. 15. A comb of the latter type is characteristic of many shrew-fleas (Smit, 1958; Traub & Barrera, 1966; Traub & Evans, 1967), and is in marked contrast to the fairly straight, pointed spines of *L. aestivalis* (Jameson & Sakaguti, 1954) (fig. 19). The spines of the comb of *L. vomerus* Traub, 1972, which is primarily a tupaiid-flea,[2] are longer and narrower (fig. 17) than in *L. ferinus*.

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[1] Unless otherwise indicated, the figures of combs herein are of male specimens.

[2] In modern schemes of classification, the tree-shrews (Tupaiidae) are either placed with the primates or as a sub-order of Insectivora (along with macroscelids), distinct from ordinary shrews and moles.

It seems surprising that a "simple" structure such as the pronotal comb should be so flexible or adaptive in evolution, and hence it is worth emphasizing that there are other genera of Siphonaptera where several kinds of pronotal combs are found within the one taxon, depending upon the host-affinities of the species concerned. For example, this is the case in *Ctenophthalmus* Kolenati, 1856, where the great majority of the approximately 100 species parasitize microtine and murid rodents, and have pronotal combs of the type shown in figs 22 and 26, viz., the spines are quite straight and broadly coming to a point apically. In contrast, in the *Ctenophthalmus* which are shrew-fleas (e.g., figs 21 and 25), the spines are generally concave and bluntly rounded apically, while mole-fleas have spines which are straight, very narrow and acutely pointed (fig. 24, and similar modifications in mole-fleas of other genera are cited by Traub & Evans, 1967). The combs of *Spalax*-infesting members of this genus (fig. 28) tend to be quite straight and fairly narrow, but not as stiletto-like as the talpid-fleas. All of the groups of *Ctenophthalmus* mentioned thus far possess combs in which the majority of the spines are definitely longer than the pronotum, but this is not the case for the few species that parasitize sciurids (*Citellus* ground-squirrels) (viz. *C. pollex* Wagner & Ioff, 1926, fig. 23). In the latter instance, the spines are proportionately shorter and broader than in the foregoing species, while the third spine from bottom (herein designated as spine number 3) is somewhat broader than the others. This last point is significant because, oddly enough, this spine is generally broad (especially at the base) in all fleas of diurnal arboreal squirrels, as will be shown. This spine is relatively broad even if those above the more dorsal ones are somewhat narrower, but usually number 2 or number 4 spine is nearly as stout as number 3.[3]

III. DATA AND OBSERVATIONS

A. The Pronotal Comb

There are other instances of taxa in which the pronotal combs of the members vary in configuration according to the host, and the number of examples that can be cited indicated that this is true convergence and is based on an actual principle. Thus, in the Holarctic ceratophyllid genus *Monopsyllus* Kolenati, 1857 (iii.1),[4] which infests a variety of cricetid and sciurid hosts, it can be seen that the spines, particularly spine number 3, are broader (especially at the base) and shorter, and fewer in number in the species illustrated in figs 62, 64 and 66, which are true fleas of diurnal tree-squirrels, than in figs 55, 57, 59 and 61, which pertain to fleas of non-sciurids. The spines of the comb of the dormouse-flea (fig. 60) and of the flying-squirrel flea (fig. 58) are also longer and narrower than those of the fleas of diurnal squirrels, and exceed them in number.

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[3] The hyperdevelopment of a single spine of the pronotal comb reaches a bizarre zenith in the pygiopsyllid genus *Traubia* Smit, 1953a. Smit described this genus on the basis of one species, and cited as a generic character the fact that the number 2 spine was much longer than its mates. Today there are 9 species of *Traubia* known to me, and all possess this odd feature, which seems to be unique in the Order. This development, however, is in a single taxon, unlike the case of the stout spines in the squirrel-fleas.

[4] The families and subfamilies are designated by Roman and Arabic numbers, e.g. iii.1, and a list of the names for these taxa are appended.

Other examples of this trend are provided in the genera *Orchopeas* Jordan, 1933 (iii.1), *Opisodasys* Jordan, 1933 (iii.1) and *Neopsylla* Wagner, 1903 (i.7), some of which parasitize arboreal sciurids while others infest other kinds of hosts. In *Orchopeas*, the spines of the squirrel-fleas (figs 29, 31, 33 and 35) are significantly broader and shorter than are those of *O. sexdentatus* (Baker, 1904) (figs 30 and 34) and *O. leucopus* (Baker, 1904), which are fleas of peromyscines. Similarly, in *Opisodasys keeni* (Baker, 1896) (fig. 43) and *O. nesiotus* Augustson, 1941 (fig. 45) which infest *Peromyscus*, the pronotal spines are noticeably longer and narrower, and the comb extends further down, than in the case of fleas of diurnal tree-squirrels (figs 44, 46 and 48). The comb of *O. pseudarctomys* (Baker, 1904) (fig. 47) is worthy of special note. Its spines are more numerous and narrower than in the case of the fleas from the diurnal squirrels, and as noted below (Section C.4), combs of this type are characteristic of fleas parasitizing nocturnal, arboreal species. In *Neopsylla*, in which the majority of the 34 species known to me infest murines or cricetines, the combs of fleas of chipmunks or ground-squirrels (figs 37, 39 and 41) bear spines that are proportionately definitely shorter and broader than in the murid-fleas (figs 38, 40 and 42).

The second principle, namely that the combs of sundry fleas of a particular kind of host tend to converge to a uniform configuration, is well shown in the fleas of arboreal or semi-arboreal squirrels. Thus, figs 1–14 illustrate the pronotal combs of 14 species of fleas of such squirrels, representing 13 genera and 3 families of fleas, and it can be seen that in all of these, the spines in general, and at least numbers 2–4 in particular, are broader and proportionately shorter than those of fleas infesting insectivores (figs 21, 24 and 25), murids (figs 49–54, 38, 40, etc.), and the peromyscine cricetids *Peromyscus* (vide figs 36 and 43), and *Neotoma* (fig. 32). For example, spine number 3 of the pronotal comb is 4·2 times as long as broad near the base in the case of *Aenigmopsylla grodekovi* Sychevsky, 1950 (fig. 9); 4·1 times in *Macrostylophora h. hastata* (Jordan & Rothschild, 1921) (fig. 14) and 3·1 for *Libyastus infestus* (Rothschild, 1908) (fig. 13), all of which are ceratophyllid squirrel-fleas, and 4·6 in *Medwayella robinsoni* (Rothschild, 1905), a pygiopsyllid from squirrels. In contrast, the ratio of the dimensions of this spine is 5·5 in *Lentistivalius ferinus* (Rothschild, 1908) (fig. 16), and 6·2 in *Ctenophthalmus* (*Alloctenus*) *cryptotis* Traub & Barrera, 1966 (fig. 20) both of which are shrew-fleas; 5·5 in *Neopsylla dispar* Jordan, 1932 (fig. 40) and 5·4 in *Stivalius cognatus bamus* Traub, 1972, both of which infest rats.

Attention is directed to the fact that in fleas of arboreal or semi-arboreal squirrels in general, and especially in those of diurnal species, pronotal spines numbers 2 and 3 are particularly broad near the base, and number 2 tends to overlap number 1 proximally, while the base of number 3 is usually very close to that of number 2 or overlaps it.

In this regard it is important to note that the greater breadth of the spines in proportion to length, which is here indicated as being characteristic of squirrel-fleas, is a relative feature, not an absolute one that can be expressed in an "average" ratio of length to width. Thus, while it is a general rule that the spines of the combs of squirrel-fleas are shorter and broader than those of fleas infesting non-sciurid hosts, it is also necessary to consider the norm for the taxon in question, for any modification of a pronotal comb must be incorporated upon an existing framework. It is

TABLE I

RELATIVE PROPORTIONS OF CERTAIN PRONOTAL SPINES OF SQUIRREL-FLEAS AS COMPARED WITH THOSE OF FLEAS OF OTHER HOSTS

Sciurid Host	Flea	Ratio* Comb/Pronotum	No. 3 Spine Length/Width	No. 3 Spine Length/Width	Ratio* Comb/Pronotum	Flea	Non-Sciurid Host
Chipmunk	*Megabothris acerbus* (Jordan, 1925)	0·9	3·5	4·4	1·1	*Megabothris quirini* (Rothschild, 1905)	*Microtus*
Chipmunk	*Monopsyllus e. eumolpi* (Rothschild, 1905)	1	3·2	5·1	1·1	*Monopsyllus thambus* (Jordan, 1929) Fig. 57	*Peromyscus*
Tree-Squirrel	*Monopsyllus vison* (Baker, 1904) Fig. 64	0·9	3·7	4·8	1·2	*Monopsyllus exilis* (Jordan, 1937) Fig. 55	*Onychomys*
Palm-Squirrel	*Nosopsyllus ceylonensis* Smit, 1953	1·4	3·7	4·6	1·3	*Nosopsyllus l. londiniensis* (Rothschild, 1903) Fig. 49	Rats
Tree-Squirrel	*Opisodasys hollandi* Traub, 1947 Fig. 44	0·7	4·8	5·5	1·1	*Opisodasys keeni* (Baker, 1896) Fig. 43	*Peromyscus*
Tree-Squirrel	*Orchopeas howardi* (Baker, 1895) Fig. 2	1·2	3·7	5·1	1·3	*Orchopeas leucopus* (Baker, 1904) Fig. 36	*Peromyscus*
Tree-Squirrel	*Orchopeas n. nepos* (Rothschild, 1905) Fig. 29	1·0	3·6	5·3	1·4	*Orchopeas neotomae* Augustson, 1943 Fig. 32	*Neotoma*
Citellus (Ground-Squirrel)	*Ctenophthalmus pollex* Wagner & Ioff, 1926 Fig. 23	1·1	5	6	1·5	*Ctenophthalmus bisoctodentatus* Kolenati, 1863 Fig. 24	Talpids
Citellus (Ground-Squirrel)	*Neopsylla inopina* (Rothschild, 1915) Fig. 39	1·2	3·5	5·2	1·4	*Neopsylla luma* Traub, 1954 Fig. 38	*Rattus*
Tree- & Ground-Squirrels	*Medwayella robinsoni* (Rothschild, 1905) Fig. 6	0·8	5·4	6·2	1·2	*Stivalius klossi* (Jordan & Roths., 1922) Fig. 20	*Rattus*
Tree-Squirrel	*Pleochaetis soberoni* Barrera, 1958 Fig. 12	1·0	3·8	5·2	1·2	*Pleochaetis mathesoni* Traub, 1950	*Peromyscus*

* Ratio: Comb/Pronotum = length of horizontal subdorsal/length of dorsal margin of notum.

patently absurd to expect a combless flea parasitizing an African ground-squirrel to develop broad spines, especially if descended from combed ancestors, for according to Dollo's Law, structures lost in the course of evolution cannot be resurrected *per se*, as discussed by Jordan in 1947 and by Traub in 1968 and 1969. Similarly, in a taxon where the pronotal spines are in general fairly narrow, the response to parasitism of squirrels could not be validly expected to equal that in *Orchopeas*, where the spines tend to be fairly broad in all species, regardless of host. In *Nosopsyllus* Jordan, 1933 the spines are quite broad, as a rule, and hence in that genus an "average" index of length to breadth would exceed the standard for *Ctenophthalmus*. The best way to examine this hypothesis, therefore, is to compare various members of genera which parasitize both sciurid and non-sciurid hosts and see if there is a significant difference. Such a comparison is presented in Table 1.[5]

From these data it can be seen that in each case, the squirrel-infesting species have pronotal spines that are significantly broader in proportion than those of its allies on other hosts. Moreover, as shown by the comparison with the length of the pronotum, which is also presented in the table, the spines of the comb of squirrel-fleas are also definitely shorter. There definitely is an inverse correlation between the length of the spines and that of the pronotum, as per what has been designated as the Principle of Totality of Mass (Traub, 1969).

Of the fleas reported from tree-squirrels, the one with the proportionately narrowest spines is the Central American ceratophyllid *Kohlsia graphis* (Rothschild, 1909). Here the number 3 spine is 4·3 times as long as broad near the base, and the dorsal spines are about 1·2 times as long as the dorsal margin of the pronotum. However, the comparable figures for the related *K. gammonsi* Traub, 1950 are 4·8 and 1·4 respectively, so there is a significantly greater relative breadth in *K. graphis*. However, it should be noted that it is not certain that the latter is truly a squirrel-flea. Apparently there are only about 24 specimens known (in all collections extant), and although virtually all of these are from squirrels (Nicaragua, Costa Rica, Panama, etc.), Tipton & Méndez (1967) could only find 16 on a total of 60 *Sciurus granatensis chiriquensis* in Panama, all of which had been carefully examined for fleas. It may be that the true host has not yet been discovered, but my belief has been that *K. graphis* has only relatively recently transferred to squirrels. Tipton & Méndez (1967) have independently come to a similar conclusion regarding *Kohlsia* Traub, 1950 in general in Panama, and state that it "may be that some of the true hosts no longer occur in this area and certain of the present hosts have been 'adopted'."

It should also be borne in mind that these differences are consistent within the taxon, i.e. the samples are representative of the comb of squirrel-fleas whether only a few members infest arboreal or semi-arboreal squirrels, e.g. 1 of 24 for *Kohlsia*, 1 or 2 of 23 for *Pleochaetis* Jordan, 1933, 1 of 12 *Paraceras* Wagner, 1916, 6 of 46 *Nosopsyllus*; or whether the majority of the species do, viz. all 28 species of *Macrostylophora* Ewing, 1929, 12 or 13 of 13 species of *Medwayella*, 8 of 11 *Orchopeas* and 16 of 22 *Monopsyllus*. An idea of the comparative differences in the proportions that

[5] Inasmuch as no *Medwayella* are known to consistently infest non-sciurids, the representative species in the table is compared with a member of a related genus.

are involved may be gained by reviewing the illustrations of sundry *Orchopeas* (figs 29–36), *Opisodasys* (figs 43–48), *Monopsyllus* (figs 55–66) and *Neopsylla* (figs 37–42).

A further illustration of the principle that the fleas of a particular kind of host tend to disport the same type of pronotal comb is provided by *Neopsylla*. It is to be noted that in the murid-species (figs 38, 40 and 42), the pronotal spines are relatively long, narrow and straight. This is characteristic of murid-fleas in general (Traub, 1968) and examples are shown in figs 49–54, depicting combs of murid-fleas from 3 families, infesting such hosts as *Mus*, *Apodemus* and subgenera of *Rattus*. Additional examples may be seen in figs 19 and 20.

B. The Pleural Arch

For an Order that is often thought of as "homogeneous," there is a surprising amount of variation on the structure of the Siphonapteran thorax, and to a considerable extent the differences represent adaptive changes and not phylogeny, as will be noted in the section on Discussion. One of the major elements involved is the so-called pleural arch, which is present and well developed in some species and reduced or absent in others, and the two extremes may at times be seen within one genus, viz, well developed in *Opisodasys hollandi* Traub, 1947 (iii.1) (fig. 87, PL.A.) and *Ceratophyllis styx* Rothschild, 1900 (iii.1) (fig. 91, PL.A.) but absent in *O. vesperalis*° [6] (Jordan, 1929) (fig. 88) and *C. arcuegens*° Holland, 1952 (fig. 90). It is fairly well developed in *Xenopsylla vexabilis* Jordan, 1925 (ix.1) (fig. 93, PL.A.) but so reduced as to be virtually absent in *X. papuensis*° (Jordan, 1933) (fig. 92, PL.A.(?)).

In each of the above instances where the pleural arch is well developed, the metathoracic region may be described as follows: There is a stout pleural rod (PL.R.) appearing as the margin between the metepisternum (MTS.) and metepimere (MTM.), arising from the dorsal portion of the base of the metacoxa and terminating at or about the ventrocaudal angle of the subquadrate lateral metanotal area (L.M.). The latter sclerite is quite well developed, e.g. longer than high, and as long as the third vinculum (VC.3) which links into it and at least several times as tall (high) as VC.3. Above the expanded dorsal apex of the pleural rod, which is at level of VC.3, or slightly lower, there is a conspicuous gap surmounted by the semi-ovate pleural arch (PL.A.). In *O. hollandi* the arch is at level of the middle of L.M. Above the pleural arch, the dorsal and caudal margins of L.M. merge and continue dorsad as the caudal margin of the metanotum (MTN.) and the base of the metanotal flange (MT.F.). The metepimere (MTM.) flanks the pleural rod and continues dorsad laterad to L.M. and then turns dorsocaudad and runs to the anterodorsal region of the first abdominal tergum (1 T.). The short thickening known as the squamulum (SQ.) serves as a good landmark for the anterodorsal region of the metepisternum.

In the two illustrated ceratophyllids which lack the pleural arch (*O. vesperalis*°, fig. 88 and *C. arcuegens*°, fig. 90), the pleural rod (PL.R.) terminates at the ventrocaudal angle of the lateral metanotal area (L.M.). In each case L.M. is narrower than in the species possessing PL.A., and in *O. vesperalis*°, L.M. bears heavily tanned internal margins and is quite ovate, while the pleural rod (PL.R.) is quite convex. In the

[6] ° denotes species in which the pleural arch is absent, or essentially so, and these are indicated thusly henceforth.

pulicid, *X. papuensis*° (fig. 92), the pleural arch at first glance seems to be missing completely, but actually is a very narrow structure (PL.A.(?)) virtually hugging the apex of the pleural rod (PL.R.) near the ventrocaudal corner of the lateral metanotal area (L.M.); the cap is almost contiguous to the rod on the sides as well as on top. L.M. is fairly large and quadrate, but smaller than in *X. vexabilis* (fig. 93). The metepisternum (MTS.) extends higher and is longer than in other members of the genus.

As can be seen in fig. 89, in the bat-flea *Nycteridopsylla eusarca*° (Dampf, 1908) (v.1), there is no sign of the pleural arch, and the lateral metanotal area (L.M.) is very narrow and longer than high. The pleural rod (PL.R.) is flat, and serves as the margin between the metepisternum (MTS.) and the metepimere (MTM.), which is not the case in some other ischnopsyllids, e.g. *Myodopsylla* Jordan & Rothschild, 1911, in which the caudal border of MTS. overlaps MTM. The two hystrichopsyllids shown in figs 85 and 86 likewise lack the pleural arch, but they present a thorax which is very different from the types described above (and differ from one another) but these are treated later, in the Discussion.

IV. DISCUSSION

A. The Function of the Pronotal Comb

1. General Comments. The modifications of the pattern of the pronotal comb consistently exhibited by shrew-fleas, bird-fleas, etc. should be adaptive, i.e. of some significant value to the insect, and the most obvious function for the specialized comb would be to serve as a device to prevent backward motion amongst the hairs or feathers of the particular host, for, as N. C. Rothschild pointed out in 1917, even non-combed fleas are unable to move backwards, thanks to the firm caudad-directed bristles of the body. Thus, the mere presence of a comb would facilitate ready *forward* passage through the hairs, but the inclination of the spines and the gaps between them would have to jibe with the structure and density of the hairs of the host before they could effectively prevent backward motion induced by teeth, beak or claws of the host intent on destroying or removing the flea. The various references cited in the Introduction include data and discussions on these points, and Humphries' articles (1966, 1967) include specific measurements showing how, in designated instances, the combs of a variety of fleas are so framed that they effectively entrap the hairs of the host in backward locomotion. Ioff, as early as 1929 tried to account for the unusual, short, pale, bluntly pointed or rounded genal spines in *Ctenophthalmus* (*Neoctenophthalmus*) *dilatatus* Wagner, 1928 in terms of the "extremely thick soft silky fur of the hosts of this flea" (the burrowing mole-rat, *Myospalax*).[7]

2. Special kinds of Combs on Fur-Fleas. In speaking of fleas which move about fairly freely in the pelage of the host, viz., the species which Ioff (1929) called

[7] Ioff (1929) also speculated that the type of genal comb in *C. dilatatus* represented an acceleration or development of the trend in this group of fleas towards variation in number and reduction in size of the spines of the genal comb. He thought this evolutionary trend might be due to the frequency of overt damage to ctenidial spines seen in these fleas. (Such broken spines are often seen in fleas of other fossorial hosts as well—R.T.)

"fur-fleas," Traub (1968) pointed out that fleas with stiletto-like pronotal spines are characteristic parasites of peramelid marsupials (bandicoots) while their close relatives on rats have bluntly pointed spines and that these ctenidia correlate well with the nature of the fur of the host. Holland (1969) also independently observed the convergence of the pointed spines seen in the pronotal comb of most bandicoot-fleas. Recent collections in New Guinea provide new data reinforcing this hypothesis. Thus, on the basis of the six species then known, Holland (1969), when describing *Papuapsylla*, understandably concluded that the pronotal spines were characteristically bluntly pointed or rounded at the apex. These species infest sundry rats, and the same is true for the minimum of eight new species of *Papuapsylla* known to me which possess a similar type of comb of broad, subrounded, slightly upcurved spines. However, two undescribed *Papuapsylla* from bandicoots have combs with spines that are straight and relatively acutely pointed, again indicating the moulding-influence of the vestiture of the host upon the flea.

Humphries (1966) well demonstrated how the pronotal spines of certain fleas (which were not squirrel-parasites) "appeared to be structured in relation to the host's hair," and there can be little doubt that the processes of natural selection have tailored the pronotal combs to conform with the host-pelage in many instances. It seems likely that this may also be the case in the fur-fleas of diurnal arboreal and semi-arboreal squirrels, for, as shown above, all the combed species exhibit essentially the same type of ctenidium, even though a variety of taxa of fleas and many genera of sciurids and four continents are involved. Not only do these combs bear relatively broad spines subventrally, but, the bases in particular are broad, and the gaps between spines number 1 and number 2 and spines number 2 and number 3 are not only acute proximally, but often overlap at the base. As a result, any hair slipping between the teeth would be grasped in a scissors-like vise if the flea were pulled backwards. Moreover, this modification seems to be at the precise height to best grasp the axil of the hairs in their normal position. However, this hypothesis needs testing by experimentation and careful measurements, for we lack such data, and further, the theory implies that the sundry squirrels have a basically similar type of vestiture, and we do not know if this is so. Nevertheless, the similarity of the hairs should not be expected to be precise, for the combs of squirrel-fleas are not fully uniform, viz, the spines in the fleas of semi-arboreal species like *Dremomys*, *Rhinosciurus*, *Lariscus* etc. are often somewhat narrower than those of fleas of truly arboreal squirrels. This can be seen in *Macrostylophora borneensis* (Jordan, 1926) (fig. 96), a flea of *Dremomys*, as compared to *M. hastata* (Jordan & Rothschild, 1921), a flea of tree-dwelling *Callosciurus*. This in turn suggests that the hairs of *Dremomys* are coarser than *C. erythraeus*. Simple comparative measurements alone will not suffice, however, for heed must be paid to the precise parts of the body of the squirrels where particular species of fleas are most apt to be found, because the sizes of the hairs vary, and so do the habits of different fleas (Traub & Evans, 1967). As those authors indicated, apparently there is limited mobility in the comb itself, so that it can be either somewhat appressed to the body or slightly removed from it, and this is another factor to consider. Certainly, however, the present writer can advance no

other hypothesis but the matching of hairs and spines to account for the convergence in the pronotal combs of the fleas of diurnal, arboreal squirrels.

Holland (1964) reported that "*Archaeopsylla* spp. (Pulicidae) and *Bradiopsylla echidnae* (Denny, 1843) (Pygiopsyllidae) share a structural modification of the pronotal comb not otherwise known in either family," referring to the fact that the ctenidium consists of only a very few spines (dorsal in position) and that these are fairly well separated, very short and are broad at the base and apically pointed. Holland then went on to say that "it may be significant that the former infest hedgehogs (*Erinaceus*) which are spiny insectivores while the latter lives on echidnas (*Tachyglossus*) which are spiny monotremes". It seems to me that this noteworthy observation really does pertain to an example of true convergence in that the nature of the comb can be explained by considering the spinose vestiture of the host. That is, the broad gap between the pronotal spines would appear to correspond with the diameter of the spines of the host, and the short pronotal spines could successfully span the mammalian spines, fitting snugly and securely against them. In contrast, a comb of long spines could not do so unless the spines were extremely divergent apically—far more so than is known in any flea, and, in fact, the apices of the spines would tend to overlap and cross one another. Moreover, the divergence between the short spines of these fleas of spiny animals presumably also accounts for the short height and dorsal position of the comb. A long comb is incompatible with subdorsal spines that are markedly divergent, for these spines would have to overlap and hence not function properly. That there is an intimate association between a short pronotal comb of small, widely spaced spines, and infestation of spiny animals is further suggested by the fact that the monotypic pulicid genus *Centetipsylla* Jordan, 1925, a parasite of Madagascar "hedgehogs" (tenrecs), has a comb of this type, while related genera, infesting non-spiny hosts, do not.

However, instances have also been cited where the relationship between comb of the flea and vestiture of the host cannot be so simple (Traub & Evans, 1967). An example of this is the "flared comb" of some shrew-fleas and macroscelid-fleas which arches back over the mesonotum, as described by these authors. Here the gap between some of the spines is inclined at nearly right angles to the longitudinal axis of the body, and hence it would be difficult for such a comb to grasp and retain hairs if the flea were in the usual position most fleas assume when feeding. However, if these particular fleas act like those noted in New Guinea which have marginal rows of spiniform bristles on the head (and/or flattened pronotal margins), and incline the body head-downwards and thus hook the hairs of the host (Traub, 1968, 1969), the flared comb may then be an effective mechanism against dislodgement. This hypothesis can be verified only by direct observation, however.

Another example of a type of comb which presumably is not directly associated with host-pelage is that characteristic of fleas found in the fur of mammals in desert areas, in which the teeth of the comb are long and narrow, are close-set at the base and point somewhat dorsad or laterad so that the apices are as remote as possible from the mesonotum (Traub & Evans, 1967). The *Orchopeas* of desert-*Neotoma* have combs of this pattern, viz, a subspecies of *O. sexdentatus* (fig. 34) and *O. neotomae*

Augustson, 1943 (fig. 32), in contrast to *O. sexdentatus agilis* (Rothschild, 1905) (fig. 30), from a mesic habitat.

3. The Pronotal Comb of Fleas of Non-Arboreal Nests. The type of pronotal comb which is most difficult to associate with host-pelage is that exhibited by certain mammal-fleas which presumably characteristically infest the nests of their hosts (usually underground or on the surface) and which are seldom found on the mammals themselves, apparently feeding while the hosts are in the nests (Traub & Evans, 1967). Examples of the combs of fleas believed to be of this type are shown in figs 67–84, 86 and 98, and it will be noted that in these the spines are much broader and generally much shorter than those indicated for squirrel-fleas (and hence far more so than in shrew- and murid-fleas, etc.). In such combs there are only 6 or 7 spines per side, instead of the usual 8–10 or more, and the spines are only 3·5–4·5 times as long as broad, instead of 5–7 times or more. Some of the number 2 spines are so stout that they are scarcely thrice as long as broad. (Amongst fleas in general there is a good correlation between a low number of spines in the comb and unusually broad girth, as compared to large numbers of spines and narrow breadths, provided the comb is of full size, i.e. extends down to near the vinculum.)

It is remarkable how large a variety of fleas, from a large assortment of hosts and from widely separated parts of the world, present essentially this type of pronotal comb. Included in the illustrations are representatives from 17 genera from 3 different families of fleas and a total of 5 subfamilies. Geographically, North America, Central America and Asia are listed, while 12 genera of hosts are cited, and these refer to 2 orders; 2 families of 1 of the orders; 3 subfamilies of cricetids and 2 tribes of cricetines.

The question immediately arises as to why fleas of such diverse backgrounds should uniformly present a single morphological feature. It seems extremely unlikely that such a variety of hosts should converge to the same type of pelage and that hence the pattern of pronotal combs represents parallel development of spines adapted to fit the hairs of the host. Thus, if the type of pronotal comb were determined purely by the type of fur of the host, then there should be no difference between the pattern of ctenidium exhibited by a flea which feeds while in the fur of an active host and that of one feeding on that host in the nest. However, frequently the nest-flea has a markedly different type of pronotal comb than the flea living in the fur of precisely the same individual mammal, e.g. the nest-flea *Conorhinopsylla nidicola*° Jellison, 1945 (i.2) (fig. 86) versus the fur-flea *Orchopeas sexdentatus* (iii.1) (figs 30, 34) on *Neotoma*; *Phalacropsylla paradisea* Rothschild, 1915 (i.7) (fig. 78), versus *O. neotomae* Augustson, 1943) (iii.1) (fig. 32), also on *Neotoma*; or nest-fleas like *Catallagia charlottensis* (Baker, 1898) (i.7) (fig. 67) and *Delotelis telegoni* (Rothschild, 1905) (i.7) (fig. 74) in contrast to fur-fleas like *Monopsyllus wagneri* (Baker, 1904) (iii.1) (fig. 59) and *Opisodasys keeni* (iii.1) (fig. 43), which infest *Peromyscus*. Most of these genera of nest-fleas do not include fleas which also infest the fur of the hosts, but *Pleochaetis* is an instructive exception. *P. paramundus* Traub, 1950 (fig. 62) is the only representative which is believed to be a nest-flea and it has relatively short and broad pronotal spines. Amongst the other 22 species, the one with the broadest spines in the comb is the

squirrel-flea, *P. soberoni* Barrera, 1958 (fig. 12) and, of course, its spines do not compare in breadth with those of the former species.

In order to explain the phenomenon of convergence of the pronotal comb to this type, it is necessary to digress and first discuss nest-fleas in general, as well as such topics as the pleural arch of the metathorax and the varying degrees of the development of the eye seen in various fleas, since morphological modification of these structures are marked in nest-fleas.

B. Nest-Fleas in General

1. Introduction. Various students of Siphonaptera have noted that certain groups of fleas are relatively seldom found on the bodies of their hosts but are nevertheless common within the nests of the mammal or bird concerned, and that these fleas are morphologically modified in various ways that reflect their pattern of life, viz., the tendency to remain in nest-litter or to crawl into cracks and crevices in the nest and to feed on their hosts while the latter are in their nests, perhaps while they are sleeping. Presumably they are found on the host only if the mammal or bird leaves the nest prematurely, as when frightened or during the breeding season, when the hosts rarely linger in the burrows, and thus the flea is interrupted in its feeding. As indicated below, the true nest-fleas differ substantially in appearance from "fur-fleas" which spend most of their time on the pelage of the host, even when active out of the nest, and are modified accordingly. However, before proceeding, it is necessary to point out that the term "nest-flea" has been used in several different senses. Ioff (1929) used it to refer to all species which were more common in the nest than on the host, even though they may have often been collected on the host, and even though they were adapted for living in the fur. Hubbard (1947) also noted that it was far easier to collect certain fleas in the nest than on the mammal. In 1941, Ioff pointed out that "fur-fleas" need frequent blood meals and apparently cannot survive if off the host for long periods, whereas the "nest-fleas" were only occasionally found on the hosts and could remain away from the mammals long enough to be able to hibernate in the nest in its absence. Ioff thus made distinctions that were physiological and ecological and of undoubted importance in the epidemiology of plague. Nevertheless, no further definition was given, and, indeed, probably would have been impossible because of the variations in degree that occur in the two groups of fleas, and because the habits of the fleas may vary with the season, etc. As will be shown, some bird-fleas feed avidly while the young are in the nest and then undergo prolonged fasting. Sazonova (1962) cited other examples of species "that feed more frequently than nest-fleas but are also able to survive for a long time in empty nests," and alludes to "such typical nest species as *Neopsylla setosa* [that] spend therefore a longer time on the host than usual" when the female fleas are maturing their eggs. For these reasons Zhovtyi (1960) validly advised against placing fleas in such ecological groups until such time as more information had been obtained about their habits, bionomics, etc. Zhovtyi later (1963) developed this theme further, and objected anew to classifying fleas into "nest" and "fur" categories, pointing out that in his view the fleas in question (*Citellophilus tesquorum* (Wagner, 1898), *Neopsylla setosa* (Wagner, 1898), *Ctenophthalmus pollex* and several species of

Xenopsylla) were all "more adapted to the nest than to the fur of their hosts and also spend more time in the nests than on the hosts themselves". An additional complicating factor was that the same species were found to be more prevalent in the nest than on the host at certain times or seasons, whereas at other times the reverse was true.

It should be borne in mind that Zhovtyi and the other Soviet authors were discussing differences in behaviour that are physiological in basis, depending upon the life cycles of the fleas (which in turn may prove to be attuned to the hormonal or physiological state of the host itself, as at times of hibernation or breeding) or, as Zhovtyi (1963) indicated, upon ecological conditions such as temperature or atmospheric humidity.

In the present paper, however, we are discussing other types (and other taxa) of fleas, e.g. those which are morphologically highly specialized for feeding upon their hosts when they are in repose in the nest, and which rarely accompany the mammal or bird out of the nest. These specially adapted fleas are herein referred to as nest-fleas because the term is convenient, has been used in the past in this sense, and because, for our purposes, it can be defined in terms of structural modifications. In this case too, it will be shown that there are varying degrees of specialization, but the concept of nest-fleas, is an important and useful one. The species called nest-fleas in the present paper are characterized by possessing several or many of the following features: (1) An eye which is rudimentary, vestigial or absent. (2) Reduction in chaetotaxy, including the numbers of rows of bristles and the numbers of bristles on various parts of the body, and in diameter of the bristles. Even the antepygidial bristles may be exceedingly few in number and/or be very thin, and even at times be present in females and absent in males, i.e. most Rhadinopsyllini. (3) Reduction in numbers of spines in combs, or the numbers of the ctenidia, or the height and length of the comb; or else the elimination of combs altogether. (4) A similar, but even more pronounced reduction in or elimination of the apical spinelets, viz., the so-called "minor combs." (5) Reduction of the thorax, including shortening of sclerites such as the lateral metanotal area; consolidation of parts; diminution in size of the pleural arch, or its loss altogether; or reduction in the degree of sclerotization of the metanotal flange, or in its size; and loss of its apical spinelets. (6) Legs relatively long and slender. (7) Lessening of the ability to jump, or concomitant increase in the facility of crawling and entering tight cracks. (8) Hyperdevelopment of certain structures, e.g. lengthening of stylets and labial palpi (at times with an increase in the number of joints), development of broadened sections of antennal segments which enclose other segments; or of lobes on the coxae, or of straight or angled anterior margins on some thoracic sterna; elongation of legs at times accompanied by development of a fringe of long bristles on the male hind tarsus. (9) Loss in degree of sclerotization of caudal margins of abdominal segments. This may be accompanied by hyper-sclerotization of the antero-dorsal portions. (10) Diminution in size. At least some of these points were mentioned by Holland, 1949, 1952, 1965; Hopkins & Rothschild, 1962; Lewis, 1969; M. Rothschild & Clay, 1952; Traub, 1950a, 1950b, 1952, 1953a, 1953b; Traub & Tipton, 1951; Traub & Barrera, 1966; Traub & Evans, 1967; and M. Rothschild, 1969. It is also apparent from the

comments by N. C. Rothschild (1917) and Jordan (1937) on Convergent Evolution, as well as from their descriptive notes on *Phalacropsylla* Rothschild, 1915, *Anomiopsyllus*° Baker, 1904 and *Callistopsyllus*° Jordan & Rothschild, 1915 (vide N. C. Rothschild, 1915; Jordan & Rothschild, 1915) that these scientists were fully cognizant of such modifications and the correlation with nest-inhabitation, although they usually did not refer to the association by name.

The known acme of specialization as nest-fleas are in forms like *Anomiopsyllus*° and *Wenzella*° Traub, 1953, which lack combs, eyes, and the pleural arch entirely, and which have long slender legs and mouthparts. Even the apical spinelets, possessed by most fleas and believed to represent vestigial combs (Traub & Evans, 1967), are missing. In the former, the species are often virtually nude, or the few bristles present are short and thin. In *Wenzella*°, the bristles are very thin, while the intercalary bristles of the abdominal rows are virtually only vestiges. In *Jordanopsylla* Traub & Tipton, 1951, this process, which has been termed "evolution by loss" or "specialization by simplification" by Hopkins & Rothschild (1962) has proceeded to the point of reduction of the eye and pleural arch, but not to their complete elimination, although the combs are absent, the mouthparts elongate, legs lengthened, etc., etc. In *Megarthroglossus*° Jordan & Rothschild, 1915 the modifications include extremely long mouthparts, coupled with reduction in the eye and vestiture, loss of pleural arch, etc. and while there is a pronotal comb, it consists of only 7–8 short, broad spines per side. Other genera possess these attributes to varying degrees, and on these grounds, as well as the fact that the species involved have rarely been collected on reported hosts, the following are cited as examples of nest-fleas. (In many instances the nests of the hosts have been insufficiently studied to permit one to state that these fleas are actually more numerous in the nest than on the birds or mammals themselves.)

2. Hystrichopsyllid Nest-Fleas. Amongst subfamilies of Hystrichopsyllidae, 7 of the 8 Anomiopsyllinae genera are deemed nest-fleas, viz.: *Anomiopsyllus*°, *Conorhinopsylla*° Stewart, 1930, *Callistopsyllus*°, *Eopsylla*° Argyropulo, 1946, *Jordanopsylla*, *Megarthroglossus*°, and *Wagnerina* Ioff & Argyropulo, 1934. The exception, *Stenistomera*° Rothschild, 1915, is discussed later as a special case. (From the ° mark, it can be seen that 6 of these genera lack the pleural arch.) Of the 7 known Rhadinopsyllinae, all of which have no pleural arch, *Rhadinopsylla*° Jordan & Rothschild, 1912, *Stenischia*° Jordan, 1932, and *Wenzella*° are regarded as nest-fleas. *Trichopsylloides*° Ewing, 1938, is probably a nest-flea, and is discussed further in Section IV.C.5. Of the 11 Neopsyllinae, at least 8 fall in the category of nest-fleas, namely, *Catallagia* Rothschild, 1915, *Delotelis* Jordan, 1937, *Epitedia* Jordan, 1938, *Genoneopsylla* Wu, Wu & Liu, 1966,[8] *Phalacropsylla*, *Paraneopsylla* Tiflov, 1937, *Strepsylla* Traub, 1950 and *Tamiophila* Jordan, 1938. (The exceptions are *Meringis* Jordan, 1937, *Neopsylla*, *Rothschildiana* Smit, 1952.) One of the 6 genera of

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[8] New Synonymy. *Evansipsylla* Traub, 1968 is a synonym of *Genoneopsylla* Wu, Wu & Liu, 1966, the description of which escaped my notice when the Chinese ceased filling subscriptions to their journals. The type-species proposed, *thysanota* Traub, 1968 is presumably different from the type of *Genoneopsylla*, namely *longisetosa* Wu, Wu & Liu, 1966, but one cannot be certain because of the lack of details in the sketches that illustrate *longisetosa*.

Ctenophthalminae seem to be a nest-flea, viz. the South American *Agastopsylla*° Jordan & Rothschild, 1923, as indicated by the marked reduction of the thorax, and in chaetotaxy, etc. It has been pointed out that the short pale spines in the genal comb, and their frequent variation in number (even on the two sides of the same specimen), all are suggestive of "an evolutionary tendency in the genus towards complete reduction of the comb" (Traub, 1952), while morphological similarities with anomiopsyllines were therein deemed examples of convergent evolution in unrelated nest-fleas.

It is possible that one of the 5 Doratopsyllinae may prove to be a nest-flea, viz. *Idilla*° Smit, 1957, an Australian marsupial-flea, in which there is rather great reduction in chaetotaxy and loss of the pleural arch. However, there seems to be little else to suggest modifications along the lines we have been discussing. The well developed genal comb and pronotal comb, plus the fact that some of the few bristles on the thorax and one on the head are unusually short and stout, lead me to believe it is specialized in another direction, as indicated in Section B.9 below.

Of unusual interest are hystrichopsyllids which possess some of the typical attributes of nest-fleas but which nevertheless bear genal and ctenidial combs, e.g. *Stenischia*°. Thus, these fleas are characterized by: reduction of the eye, thorax (including loss of the pleural arch), and chaetotaxy; long, slender legs; development of heavy incrassations on the dorsal margins of the abdominal terga and ventral margins of the sterna, coupled with unusually lightly tanned median portions of these segments—all features associated with nest-fleas. Here too, in my opinion, the ctenidia are reduced, but the term is a relative one, in that what appears to be well developed combs in reality probably represents a marked diminution in the size and number of spines borne by their ancestors, or by related taxa such as *Nearctopsylla* Rothschild, 1915, which have much more pronounced combs. This point is considered further in Sections IV.C.2 and IV.E below.

3. Pygiopsyllid Nest-Fleas. Amongst the pygiopsyllids, there are only very few instances where fleas seem to have assumed the nest-habit. One is *Choristopsylla tristis*° (Rothschild, 1900), which, even more than other members of its genus, has reduced chaetotaxy (essentially only 1 row of bristles on abdominal terga and those very slender); long slender legs, with metatarsus I particularly long; the pleural arch so reduced as to be essentially absent; lateral metanotal area small, etc. Remarkable parallel developments between this flea and those of fleas of Nearctic flying-squirrels (and their hosts too) are mentioned later. Two other pygiopsyllids which are likely candidates, despite the presence of a pleural arch, are the monotypic *Lycopsylla* Rothschild, 1904 (Australia and Tasmania, on wombats) and *Notiopsylla* Jordan & Rothschild, 1914 (2 species, 1 ex procellariiform sea-birds; the other apparently from a parakeet that spends most of its time on the ground; both on sub-antarctic islands). Both of these genera are combless, a highly unusual condition amongst pygiopsyllids, and the lateral metanotal area is narrow. However, *Notiopsylla* is clothed with many fine hairs, suggesting it may spend some time on the host as well as in the burrows. The scanty records indicate this is so for *N. kergue-*

lensis (Taschenberg, 1880), but *N. enciari* Smit, 1957 is apparently known only from a very few specimens and hence data are lacking.

Lycopsylla shows marked reduction of chaetotaxy (both in numbers and size of bristles), but the pleural arch is better developed than in known nest-fleas. As will be shown, the size of the pleural arch is correlated with jumping ability, and since fleas of large mammals tend to be excellent jumpers (e.g. *Ctenocephalides* Stiles & Collins, 1930), and the wombat grows to a size of about 1200 mm in length and about 800 mm in height (more than 20 inches tall), it is not surprising that this flea does not show much reduction of the thorax

4. CERATOPHYLLID NEST-FLEAS. Nest-fleas occur in the Ceratophyllidae too, although they are of much less frequent occurrence than in the Hystochopsyllidae. Among the classic examples are a relatively few species of the large genus *Ceratophyllus* Curtis, 1832, such as the Nearctic *C. arcuegens*° (fig. 90), and the Palaearctic *C. rusticus*° Wagner, 1903, *C. caliotes*° Jordan, 1937 and *C. orites*° Jordan, 1937, in which there is reduced chaetotaxy, loss of the pleural arch, development of slender legs, etc. (Holland, 1952; M. Rothschild, 1969). *C. delichoni*° Nordberg, 1935, also belongs in this category, as can be seen from Smit's excellent re-description (1956). These fleas parasitize martins and cliff swallows, but there are also other species of *Ceratophyllus* that infest these particular birds, e.g. *C. styx* (fig. 91), and yet which lack most or all the morphological modifications of the *C. arcuegens*-group, as can be seen by comparing figs 90 and 91. This is discussed below, when it is pointed out that these bird-nest fleas have well developed eyes, unlike the case in fleas of mammal-nests.

Perhaps the most remarkable bird-flea is the Antarctic *Glaciopsyllus antarcticus*° Smit & Dunnet, 1962, which lives in the nest of the snow-petrel, often under many feet of snow (Murray et al., 1967). This flea is so specialized that it has not only lost the pleural arch but the pronotal comb as well (and is thereby unique in the family), and shows the reduced chaetotaxy, slender legs and other nest-flea features, but here again the eye is large. Amongst ceratophyllids of mammals that seem to be nest-fleas, may be mentioned *Syngenopsyllus*° Traub, 1950 (Indo-Malaysian), *Libyastus*° Jordan, 1936 (African), *Tarsopsylla*° Wagner, 1927 (Holarctic), all of which are fleas of tree-squirrels (or their nests) and *Hollandipsylla*° Traub, 1953, from a Bornean flying-squirrel. I believe that to a considerable extent the following ceratophyllid fleas spend much of their time in the nest rather than on the host, viz., the 2 species of *Opisodasys* which parasitize flying-squirrels, *O. pseudarctomys*° and *O. vesperalis*° (but not the rest of the species of *Opisodasys*, which infest tree-squirrels and *Peromyscus*); the dormouse-flea, *Myoxopsylla*° Wagner, 1927; the Mexican *Pleochaetis paramundus*, which is a *Neotomodon*-flea (but not the remaining 22 species of *Pleochaetis*, which infest primarily *Peromyscus*); and the Palaearctic marmot-flea *Callopsylla dolabris* (Jordan & Rothschild, 1911).

The ceratophyllid nest-fleas, especially those of mammals, are not as modified morphologically as are the bulk of the hystrichopsyllids, etc. However, all of those listed, save *P. paramundus* and *C. dolabris*, lack the pleural arch, but in the last 2, the arch is smaller than in their relatives, and the latter especially show other thoracic

changes, such as a narrowing and deepening of the lateral metanotal area. All tend to have reduced eyes and have fewer and thinner bristles; and more slender and elongate mouthparts and legs; and a narrower metepimere (except for *P. paramundus*), than do their allies which infest the fur of their hosts. The more specialized thoracic differences may be seen by comparing fig. 87 (*O. hollandi*, a fur-flea of diurnal tree-squirrels) and fig. 88 (*O. vesperalis*°). The maximum degree of relevant differentiation in the family may be seen by contrasting the head and thorax of *C. arcuegens*° (fig. 90) with that of *C. styx* (fig. 91). There is an odd species ascribed to the Ceratophyllidae which may prove to be a nest-flea, namely *Brevictenidia mikulini* (Schwarz, 1960), the sole representative of the genus (and which I have not seen). This is characterized by a pronotal comb of "vestigial" widely-spaced, acuminate spines which are less than ½ the length of the pronotum. The elongate palpi, the very small eye, and reduced chaetotaxy shown in the published figures (Liu & Li, 1965) parallel the modifications indicated above. There is some doubt about whether this really is a ceratophyllid or leptopsyllid.

5. LEPTOPSYLLID NEST-FLEAS. There are few nest-fleas known in the Leptopsyllidae, but these exhibit the same tendencies. Thus, *Brachyctenonotus*° Wagner, 1928, a monotypic genus parasitizing mole-rats in south central Asia, not only lacks the pleural arch and has a very reduced eye, but its pronotal comb consists of extremely short and broad spines. Allied to *Brachyctenonotus*° is the monotypic genus *Calceopsylla*° Liu, Wu & Wang, 1965, which judging from the figures and English summary of the original description (Liu, Wu & Wang, 1965), is a typical nest-flea since the eye is absent, the palpi elongate, the pronotal comb markedly reduced, the pleural arch missing, the abdominal spinelets absent, etc. The spines of the comb are narrow, very short and widely spaced, as in the former genus. *Phaenopsylla* Jordan, 1944, *Hopkinsipsylla* Traub, 1963 and *Paradoxopsyllus microphthalmus* Ioff, 1946, although possessing the pleural arch, conform to the picture that is now familiar through repetition.

An instructive stage in the development towards the nest-flea habitus is seen in *Amphipsylla marikovskii* Ioff & Tiflov, 1939. In ordinary species of *Amphipsylla* Wagner, 1909, the eye is quite small; there are about 20 spines (total) in the pronotal comb, the pleural arch is well developed, the lateral metanotal area is relatively broad, and the false combs of bristles on the pro- and metatibiae are generally prominent. In *A. montana* Argyropulo, 1946, for example, it may be noted that spines numbers 2–4 of the pronotal comb (fig. 105) are fairly straight and number 3 is more than 5 times as long as broad; the tanned margins of the pleural arch (PL.A.) extends well below the apex of the pleural rod (PL.R.); the gap between the arch and the tip of the rod exceeds the girth of the dorsal part of the rod; the lateral metanotal area (L.M.) is only about 1·3 times as long as tall and scarcely extends beyond the pleural rod; there is a false comb of 8 short, stiff, straight, somewhat spiniform bristles on the protibia (fig. 103) and one of about 6–8 such modified bristles on the metatibia (fig. 104). In contrast, in *A. marikovskii*, the eye is almost vestigial; there are only about 16 spines in the pronotal comb (fig. 100), spines numbers 3–5 are dorsally concave and relatively broad, e.g. number 3 is about 3·8 times as long as broad at the

base; the pleural arch (PL.A.) is greatly reduced, viz., it is very small and compact, scarcely broader than the apex of the pleural rod (PL.R.) and almost contiguous with it; the lateral metanotal area is somewhat narrowed, viz., about 1·5 times as long and extends well caudad of the rod; the false comb on the protibia (fig. 101) consists of only 4 straight bristles and that of the metatibia (fig. 102) of but 3 bristles and these are inclined more ventrad than in unmodified members of the genus.

An earlier step in this evolutionary trend is illustrated by fig. 94, showing the head and thorax of *Ophthalmopsylla* (*Eremedosa*) *celata* Traub, 1965 compared with that of *O. jettmari* Jordan, 1929, which is not a nest-flea (fig. 95). It is apparent that in *O. celata*, the eye is greatly reduced, the bristles are far fewer in number and are significantly more slender; the lateral metanotal area (L.M.) and metepimere (MTM.) narrower, the pleural arch (PL.A.) smaller and narrower, etc. There are fewer spines in the pronotal comb, but here *O. celata* has not progressed as far as *Phaenopsylla* (vide fig. 80), which has also become more specialized in other respects, viz., the eye is vestigial.

6. Pulicid Nest-Fleas. Nest-fleas are rare in the Pulicidae, and it seems highly significant that the only such mammal-flea known to me, *Xenopsylla papuensis*°, a parasite of *Pogonomys* in New Guinea, conforms closely to the pattern and may be unique amongst the 70 described species in the genus in lacking a true pleural arch. Actually, the pleural arch is present in vestigial form (PL.A.(?)), arising from the ventrocaudal angle of the lateral metanotal area (L.M.), but it is extremely short and narrow, and is virtually contiguous with the top of the pleural rod, especially in the male. Like all *Xenopsylla* Glinkiewicz, 1907, it is combless, but as can be seen by comparing fig. 92 with fig. 93 (a New Guinean specimen of the related *X. vexabilis*, a fur-parasite of rats), the eye is absent in the former species, instead of being quite well developed; there are fewer bristles on the head and on the metepimere (MTM.), e.g. 2–4 instead of 5–5; the bristles in general are distinctly narrower; and MTM. is relatively narrow.

In the California pulicid flea of sea-birds, *Actenopsylla suavis* Jordan & Rothschild, 1923, there is a very small pleural arch and the lateral metanotal area is narrow, recalling the condition in some other fleas of sea-birds, and the accompanying reduction of the eye (fig. 99) and the chaetotaxy suggest that the flea spends much of its time in the nest-habitat of its host (*Ptychorhamphus*), which is in burrows in the ground. It seems significant that this flea, and its ally, *Ornithopsylla laetitiae* Rothschild, 1908, the only bird-fleas in the group, are likewise the only members of the tribe lacking genal and pronotal ctenidia. The latter is also a flea of sea-birds (*Puffinus*), and has been found in their nests as well as on the bodies of the hosts, and is modified along somewhat similar morphological lines as *Actenopsylla* Jordan & Rothschild, 1923. However, the straight frontal margin of the head of *Ornithopsylla* Rothschild, 1908 and the somewhat larger eye, lead me to believe that it is not as much of a nest-inhabitant as the former.

7. Chimaeropsyllid Nest-fleas. The small family Chimaeropsyllidae is limited to the Ethiopian Region and primarily to South Africa. The majority of the

species of the largest genus, *Chiastopsylla* Rothschild, 1910 (xi.2) are definitely stated to be nest-fleas, e.g. all members of the *numae*-group and especially *C. numae* (Rothschild, 1904) and *C. quadrisetis* de Meillon, 1930, and at least 5 of the 8 species in the *mulleri*-group, namely those found in the nests of *Otomys unisulcatus*, the Karoo rat (de Meillon, Davis & Hardy, 1961; Haeselbarth, 1966). *Chiastopsylla* reminds one of *Anomiopsyllus*° because of the diminutive size of the species and the marked reduction in chaetotaxy. However, unlike the latter, *Chiastopsylla* does have combs, both genal and pronotal. Significantly, though, the pronotal comb is greatly reduced and usually consists of only 5–7 short spines per side, and the genal comb at most consists of 2 spines, and at times only 1, and may be missing altogether, as in *C. pitchfordi* Ingram, 1927. Such variability of numbers of spines suggest the structures are in the process of elimination in the course of evolution. The maxillary palpi are relatively long and thin, and in *C. pitchfordi* extend to near the apex of the trochanters, and the eye is vestigial. The pleural arch is present, but is very small. The known ultimate in this line of development in the family is in the monotypic genus *Praopsylla* Ingram, 1927, which lacks combs entirely, and in which the eye is so reduced that it is represented by a mere small tanned patch. The head has an unusual subconical appearance at the frontal angle due to the anterior excision of the ventral margin, a configuration that can be seen in some other nest-fleas, e.g. *Eopsylla*° (i.2) and *Conorhinopsylla*° (i.2), (fig. 86) while the mouthparts are elongate, extending beyond the apex of the fore trochanters, the pleural arch is very small, and there is but a single row of bristles, and even the bristles on the hind tarsi are unusually short. Superficially *Cryptopsylla* de Meillon, 1949 resembles these nest-fleas, but consideration of this is best deferred.

8. Rhopalopsyllid Nest-fleas. Members of the family Rhopalopsyllidae are essentially Neotropical rodent-fleas, with a few exceptional members occurring in the subantarctic region or in southern U.S. and with some infesting birds or other hosts. Many new species, and perhaps undescribed genera, undoubtedly await discovery, for most of South America is still unexplored concerning fleas. None of the species bear true ctenidia (Traub, 1968) and one cannot discuss such modifications when considering nest-fleas. However, a number of forms exhibit reduced chaetotaxy (regarding numbers of rows, diameters), lengthened palpi and an unusually large (and variable) number of palpal segments, e.g. *Ectinorus polymerus* Jordan, 1942 and *Dysmicus barrerai* (Jordan, 1939). It therefore seems significant that Jordan (1942) cites these as being found in the nests of their hosts (*Octomys*), or, in the case of the latter species, flourishing there. The features of other related taxa suggest they too may be nest-inhabitants to a degree, and for example, de Meillon (1952) states that "*Parapsyllus* . . . is essentially a nest-flea", but on the whole too little is known about the fauna, and their habits, for further discussion.

9. Differences in degree of the Nest-flea Habitus. It is therefore clear that the development of the nest-flea habitus and habit has occurred independently many times within the Order, viz., in at least 7 families, and in 5 subfamilies of one of these, the hystrichopsyllids. However, it is emphasized that the degree of con-

vergence or differentiation varies. *Jordanopsylla* lacks combs but has a pleural arch; some have a short comb but no pleural arch; neopsyllids are quite small in size while the squirrel-fleas are of fair size, etc. It seems that some species, like *P. paramundus* (fig. 68), are relatively late entries in this line of development, and still may be found in fair number on the bodies of the host, and these tend to show a lesser degree of specialization by reduction, e.g. the eye is definitely smaller in *P. paramundus* than in other *Pleochaetis*, but it is not vestigial, and the pronotal spines are short as compared with the pronotum and are relatively quite broad, but the comb is not as modified as in *Strepsylla* (fig. 79) and *Epitedia* (fig. 77), etc. Other species of genera of nest-fleas have been extremely difficult to collect unless and until one has the opportunity to examine the nests of the hosts, as was the case with *Hopkinsipsylla* (Traub, 1963, 1965). This has also been the experience with *Tamiophila*, *Phalacropsylla* etc., while others have remained "rare" despite intensive collection of mammals in the endemic habitat, presumably because it has not been possible to seek or find the nest of the host, as happened with *Jordanopsylla* and the subgenus *Eremedosa*.

Certain genera of Siphonaptera possess some of the attributes of nest-fleas but have other characteristics which suggest that these fleas are not merely specialized to crawl about in the nest and feed on sleeping hosts. It appears that some of these species are progressing towards the nest-habit, while others may be evolving away from it, and these are herein referred to as *partial nest-fleas*. Such evolutionary manifestations are not surprising, since it seems logical to believe that the Order arose from a non-parasitic ancestor which lived in the nests of mammals or proto-mammals, feeding on organic debris, and later, perhaps, on scurf on the bodies of the residents, and gradually acquiring the facility to feed on the blood of what were by then their hosts. Development of the ectoparasitic habit was accompanied by the adaptations of making it more and more successful, e.g. flattening of the body, presence of rows of stiff backward projecting bristles or combs of spines; development of jumping legs (N. C. Rothschild, 1917; Ioff, 1929; M. Rothschild & Clay, 1952; Traub, 1966); modification of the flight mechanism into a device for leaping (Neville & M. Rothschild, 1967; M. Rothschild, 1969). It is believed that most (but not all) of the early fleas possessed many combs of spines and that most of these ctenidia have become vestigial or lost (at times with scarcely any trace) as the fleas developed other means of remaining safely on the host despite its exertions in running, or flying, or special efforts to destroy the flea by teeth, beak or claw (Traub & Barrera, 1966; Traub & Evans, 1967; Traub, 1968, 1969). Some of these new mechanisms include "false combs" of bristles to replace the true combs which had been lost (Traub, 1968). It therefore appears that the "specialization by simplification" (Hopkins & Rothschild, 1962) of nest-fleas is indeed just that, a series of modifications enabling the flea to return to a nest-existence, but in a manner superior to that of its forebears. However, in some instances, superimposed upon the model characterized by reduction of the combs and bristles, etc., are later or concurrent adaptations which enable the flea to remain on the host when it is active in the nest or burrow, or even outside, while running, leaping, gliding or flying.

An example of a taxon of fleas with such a "dual-purpose" set of modifications is the anomiopsylline hystrichopsyllid *Stenistomera*°, known from 3 species in the Nearctic deserts. Here the eye is vestigial and marked modification of the thorax accompanied the loss of the pleural arch (i.e. absence of the lateral metanotal area) and there is reduction in abdominal chaetotaxy (but one row of tergal and sternal bristles, and with intercalaries vestigial), while the legs are long and slender. However, this picture of a typical nest-flea is confused by features illustrating another evolutionary trend, which is exhibited in non-nest fleas representing such diverse taxa as some (but not all) species of *Jellisonia* Traub, 1944 and *Kohlsia*, which are ceratophyllids, and by the leptosyllids *Amphipsylla*, *Caenopsylla* Rothschild, 1909, *Ctenophyllus* Wagner, 1927, and *Peromyscopsylla* I. Fox, 1939, and by pygiopsyllids like certain *Metastivalius* Holland, 1969. These are the *combination* of: (1) A narrowed frontal region on the head (i.e. it is taller than long and often bullet-shaped); (2) A frontal margin that is somewhat flattened for the ventral half. (3) A row of frontal bristles bordering the anterior margin. (4) Tendency for bristles of the first row to be thickened near the base, or, somewhat spiniform. (5) Presence of a "false comb", i.e. a vertical row of single, short or stiff bristles, on the tibiae. (6) A full pronotal comb of many, narrow spines, with the lowest spine (or additional ones) extending over the vinculum. Modifications of the frontal margin of the head in this manner is deemed by me to be characteristic of fleas which become temporarily rather sedentary and cling to the host by hooking the marginal row of subspiniforms or thickened bristles onto the hairs while the flea abuts its head against the skin (Traub, 1968, 1969). It is noteworthy that in *Stenistomera*° only *S. alpina*° (Baker, 1895) exhibits all of these "secondary" features. In *S. macrodactyla*° Good, 1942, the first row of frontal bristles is not so marginal nor subspiniform; the tibial combs not so well developed, etc., while *S. hubbardi*° Egoscue, 1968 is intermediate. It would seem that *S. alpina*° is adapted both to feed on the host while it is in the nest and to cling successfully to the fur while the *Neotoma* is outside, where a fall from the host might mean death for a nest-flea, as stressed below (Section IV.C.2).

In the category of a flea apparently following two lines of evolution simultaneously, viz. specialization by reduction complemented by elaboration of existing structures, is the South African monotypic genus *Cryptopsylla* (xi.2). It superficially resembles the related *Praopsylla*, which presumably is a true nest-flea, in that there is no sign of a comb, but the eye is even more reduced—it is completely absent. However, there are significant differences in that the mouthparts are much shorter, there is a false comb of modified bristles on all the tibiae, and while there is but one row of abdominal bristles, these are unusually long. This is a flea of a burrowing rodent with mole-like habits, the bathyergid *Cryptomys*, and I believe the loss of the eye and development of unusually long bristles is characteristic of fleas of such hosts (i.e. *Dactylopsylla* Jordan, 1929 (iii.2) of Nearctic pocket-gophers; *Dinopsyllus* (*Cryptoctenopsyllus*) *ingens* (Rothschild, 1900) (i.4), a flea of the mole-rat *Bathyergus*). Such a coat of long thin bristles (coupled with marked reduction of the eye) is also seen in the 4 genera of fleas parasitizing *Aplodontia*, a North American rodent which spends much of its time burrowing. It seems likely that vestiture of this type not

only may help the flea stay on its host while the latter brushes against the walls of its tunnels, and that the close proximity, great length and overlapping condition of the bristles also offer protection against the grains of soil that would otherwise dust and adhere to the flea in such an environment. Since *Cryptopsylla* not only has chaetotaxy of this pattern, but also is adorned with tibial combs, I believe it spends time on its host as well as in the nest.

Other examples of fleas which have some of the attributes of nest-fleas, but not many, and which have been collected in rodent nests are *Xiphiopsylla* Jordan & Rothschild, 1913 and *Coptopsylla* Jordan & Rothschild, 1908. *Xiphiopsylla*, a genus infesting primarily rodents in the Ethiopian Region, is sufficiently distinctive to be placed in a family by itself, and the features relevant to this discussion include a vestigial eye, long thin maxillary palpi, a short pronotal comb of short spines (and hence pronotum greatly exceeding length of spines); a reduced pleural arch (virtually vestigial in *X. hyparetes* Jordan & Rothschild, 1913); a narrow metepimere and fairly slender legs. However, there are 2 or more full rows of abdominal bristles on the terga, and the long bristles are remarkable in being sword-shaped, i.e. virtually straight from base to near apex instead of tapering in the usual way. The body surface is heavily sclerotized, reticulated, sculptured or microspiculose, and there often are dorsal incrassations on the terga. The body ornamentation and the densely tanned nota may be regarded as adaptations for protection against being crushed or caught by the host, but likewise would be of value when squeezing into crevices in the nest of the host, and the stiff bristles and reticulated surfaces would facilitate crawling into tight cracks and offer resistance to being pulled out therefrom. Similar incrassations are seen in some hystrichopsyllids like *Xenodaeria* Jordan, 1932 (Doratopsyllinae), *Rothschildiana* (Neopsyllinae), the rhadinopsylline *Stenischia*° Jordan, 1932 and *Corypsylla*° C. Fox, 1908, and are examples of convergence. *Rothschildiana* also bears comblike bristles on the sterna, and the body is rigid, with the surface spiculose. These specializations suggest it likewise hides in narrow apertures in the nest.

Coptopsylla likewise is the sole representative of a special family, and is a desert flea in the southwestern subregion of the Palaearctic Region. It is strongly reminiscent of true nest-fleas in the absence of any combs, in the extreme length of the palpi and stylets; the tall, narrow lateral metanotal area, and the presence of but a single row of abdominal bristles. However, there is a well developed pleural arch, a large eye and the bristles are long, and these indicate a flea that spends at least part of the time on an active host, and as we shall see, is a good jumper and is active in the daylight.

Additional points about fleas which might be nest-fleas to a degree will be deferred until a discussion of the absence of the pleural arch and the reduction of the eyes in Siphonaptera.

Inasmuch as so many of the nest-fleas have been indicated as having lost the pleural arch and possessing reduced or vestigial eyes, these points are discussed below, since other types of fleas are so modified as well.

C. The Pleural Arch of the Metathorax

1. Review of Taxa Lacking a Pleural Arch. The absence of the pleural arch of the metathorax in certain fleas (e.g. figs 85, 86, 90, 92) is of interest and significance and constitutes another good example of Convergent Evolution in fleas, since the condition occurs in a fairly large number of genera which are often unrelated, while close allies have normal pleural arches (figs 87, 91, 93, PL.A.) (Traub, 1953b). At times, only one or two members of a large genus are affected, e.g. *Xenopsylla*, and loss or marked reduction of this structure is known in at least 6 families (Hystrichopsyllidae, Pygiopsyllidae, Ceratophyllidae, Leptopsyllidae, Ischnopsyllidae and Pulicidae) although it is quite rare in the pygiopsyllids, leptopsyllids and pulicids. Further, fleas with this trait are found in a variety of habitats in widely separated geographic areas. Ceratophyllid squirrel-fleas with the thorax modified in this manner were listed by Traub (1950, 1953), viz.: *Tarsopsylla*°[9] (Holarctic), *Syngenopsyllus*° (Indo-Malaysian), *Libyastus*° (Ethiopian), the 2 species of *Opisodasys* Jordan, 1933 which parasitize Nearctic flying-squirrels, viz. *O. pseudarctomys*° (fig. 47) and *O. vesperalis*° (fig. 88) and the monotypic Bornean flying-squirrel flea *Hollandipsylla*°. A small minority of ceratophyllid bird-fleas lack the pleural arch (Holland, 1952; M. Rothschild, 1969) i.e. *Ceratophyllus arcuegens*° (fig. 90) and the 3 other martin and bank-swallow fleas mentioned above, as well as the notable Antarctic flea, *Glaciopsyllus antarcticus*°. The arch is likewise missing in the ceratophyllid dormouse-fleas *Myoxopsylla*° and in the leptopsyllids *Brachyctenonotus*° and *Calceopsylla*°. A leptopsyllid in which the arch is greatly reduced but still discernable is *Amphipsylla marikovskii*. Among hystrichopsyllids, most anomiopsyllines (e.g. *Anomiopsyllus*°, *Megarthroglossus*°, *Conorhinopsylla*°, *Callistopsyllus*°, *Stenistomera*° and *Eopsylla*°) lack the pleural arch (Traub & Tipton, 1951) as do nearly all rhadinopsyllines (e.g. *Rhadinopsylla*°, *Corypsylla*°, *Trichopsylloides*° Ewing, 1938, *Paratyphloceras*° Ewing, 1940, *Stenischia*° and *Wenzella*°). When present in this subfamily (*Nearctopsylla* Rothschild, 1915), it is very small and the associated pleural rod is abbreviated. In neopsyllines, the pleural arch is definitely reduced in *Phalacropsylla, Genoneopsylla, Delotelis, Epitedia faceta* (Rothschild, 1915), *Tamiophila* and somewhat less as in *Strepsylla, Meringis, Catallagia* and *Paraneopsylla* as compared to *Neopsylla.* Amongst ctenophthalmines, the arch is absent in *Agastopsylla*°. Among the doratopsyllines, *Idilla*°, a monotypic genus known from dasyurine and peramelid marsupials, is similarly modified.

The arch is absent in many ischnopsyllids (bat-fleas) i.e. *Thaumapsylla*° Rothschild, 1907, *Lagaropsylla*° Jordan & Rothschild, 1921, *Araeopsylla*° Jordan & Rothschild, 1921, *Nycteridopsylla*° Oudemans, 1906 (fig. 89), etc. and is greatly reduced in *Ischnopsyllus* Westwood, 1833, *Oxyparius* Jordan, 1936 and others. Amongst pulicids, *X. papuensis*° has a thorax essentially of this type (fig. 92), thereby differing from its many allies (e.g. fig. 93). This structure is much reduced in *Rhynchopsyllus* Haller, 1880 and *Hectopsylla* Frauenfeld, 1860, which are sticktight fleas infesting birds or bats, and is also very small in male *Tunga* Jarocki, 1838 and virtually absent in female *Tunga*. These particular sticktight and burrowing fleas are at times placed

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[9] It is reiterated that the species which are marked ° in this article, lack the pleural arch.

in the family Tungidae but are regarded by some as a subfamily of Pulicidae. *Choristopsylla tristis*° is one of the few pygiopsyllids known to lack the pleural arch. Another is *Pygiopsylla celebensis*° Ewing, 1924, represented by but one specimen extant and with unknown affinities and host relationships.

Although the above review does not purport to be complete, it is clear that reduction of the thorax and loss of the pleural arch has occurred repeatedly and often sporadically throughout the Order, and without much regard for taxonomy. The important question is, what is the significance of this evolutionary development? Unless one wants to believe that an Order may have a built-in mechanism for the haphazard appearance of a single-type mutation or atavism, there ought to be a common factor or basis for such repeated but natural selection of an unusual trait. Moreover, the first possibility is ruled out since the loss of the pleural arch is accomplished in several different ways, as will be shown. In short, this trait should be adaptive or at least fit with known evolutionary principles, and in what follows an attempt will be made to demonstrate that this is indeed the case.

2. The Adaptive Value of the Loss of the Pleural Arch. A review of the list of fleas with this type of thorax, made in an attempt to determine the possible value of the modification, immediately leads to some generalizations. One is that virtually all have reduced eyes. However, the relatively few exceptions have unusually large eyes, so apparently that phenomenon is complex, and hence it will be treated later, separately, in Section IV.D.1. It is also evident that most of the names are familiar in that they were mentioned above as nest-fleas. Nevertheless, there is one glaring addition—the bat-fleas, and these provide a clue as to the function of the reduced arch, as shown below.

Various workers were impressed by the high incidence of the reduction of loss of the pleural arch in nest-fleas, and postulated that it was associated with the lessening or loss of the ability to jump well, or with sedentary habits (Traub, 1953). Apparently, the first direct statement to this effect was made by Holland (1952) when describing his new bird-flea, *Ceratophyllus arcuegens*°. He noted that, like 3 Palaearctic members of the genus (out of the many *Ceratophyllus* known), this species lacked a pleural arch (fig. 90), and went on to state that because of the reduction of the legs and thorax, and as indicated by the "rather large and deep abdomen," this was "evidently a rather sedentary species . . . ; a crawler rather than a jumper." Earlier, without specifically mentioning the loss of the pleural arch, Holland (1949), in referring to *Tarsopsylla*°, stated that "in spite of its long legs, [it] appears to be a rather sluggish flea." Smit (1953b) made similar observations regarding *Tarsopsylla*°, but again without reference to the arch, declaring "It seems to be a general rule in fleas that the ones with long and slender legs are walkers and climbers rather than jumpers, while those with stout and relatively short legs seem to be the jumping champions". Johnson (1957) discussed various modifications of the lateral metanotal area and the pleural arch, and stated she believed the latter was "mainly an aid in jumping". Johnson also indicated that "prior loss of the pleural arch is somehow connected with incorporation of the lateral metanotal area into the notum or to its complete loss". Smit & Dunnet (1962) expressed the view that *G. antarc-*

ticus° was a crawling flea, a point that was verified later by field observations (Murray et al., 1967). Traub & Evans (1967) regarded the modifications of nest-fleas, including reduction in jumping ability, as adaptations for feeding on a quiescent or sleeping host, but the true significance of the loss of the pleural arch became clear only after the brilliant work of M. Rothschild and colleagues. The pleural arch of fleas was shown to be the site of a cap-shaped mass of resilin, "an elastic protein which stores and releases energy more efficiently than any known rubber, and which can deliver power faster than most efficiently contracting muscle." (M. Rothschild, 1969.) The pleural arch of fleas is homologous with the hinge-ligament of the wing of flying insects, which is situated on the top of the pleural ridge of scorpion-flies, locusts, etc., and consists of resilin (Neville & Rothschild, 1967). The latter authors referred to fleas as "insects that fly with their legs" since the jump is effected by a modified flight-mechanism. Reduction or loss of the pleural arch, then, can only be associated with lessened ability to jump.

What advantage from loss of the arch results to fleas like *Megarthroglossus*°, *Stenistomera*° or *Conorhinopsylla*° in a nest of *Neotoma* on the ground or in a rock-ledge, or *Callistopsyllus*° in an underground nest of *Peromyscus*? As already indicated, these fleas are seldom found on rodents away from the nest, presumably not only because they are morphologically and physiologically adapted for feeding on the host while it is resting or sleeping, but because they are so ill-fitted to escape falling off an active host or being killed by it. It seems eminently logical to believe that they are not equipped to survive the external environment outside the nest, and probably neither are the eggs nor larvae. Further, most of the species cited are desert-species, and it probably is no coincidence that a large proportion of nest-fleas are species infesting mammals living in xeric areas.

Bearing in mind that nest-fleas are essentially blind and keyed to living in the dark confines of the nest, it is clear that a nest-flea which was a good jumper might, in one leap, end up in an extremely hostile environment just a few inches away from the nest. Moreover, such a flea would be unlikely to find its way back. Darskaya (1955) noted that the desert-flea *Xenopsylla gerbilli caspica* Ioff, 1950 (ix.1) dies quickly if it misses in an attempt to attach to a passing host and fails to return to the burrow promptly. Since this is not a nest-flea, and is adapted to conditions at the burrow-entrance, it is no doubt hardier regarding environmental factors than a species attuned to the microclimate deep in the rodent nest. Another disadvantage to a nest-flea of being a good jumper would be the injuries sustained in leaping about blindly in closely confined quarters. A jumper would not be very likely to crawl within the relatively favourable runway of the host if it fell off the rodent, and instead would leap into an alien world. Thus, survival in the nest-flea would be most favoured in the poor jumper and natural selection would in time lead to the reduction and loss of the pleural arch so characteristic of nest-fleas. There is then, much more to the evolution of a thorax without a pleural arch than the mere "lack of need" for effective leaps in a species of flea living in underground nests.

The adaptive value of this development is further indicated by the fact that the loss of the arch is commonly seen in nest-fleas inhabiting nests or roosts at high altitudes, e.g. squirrel-nests on tall trees, bird-nests on cliffs or in banks, or in caves, or crannies

in a tall cave where bats cling, or in holes where bats roost. As Dr Miriam Rothschild has pointed out in the lecture summarized by Neville & M. Rothschild (1967) a leap of 10–12", the type readily accomplished by a flea with a well developed pleural arch, could carry an aerial nest-flea 100 feet down and away from the host it is dependent upon for the blood-meal necessary for nourishment and to prime egg-laying. The selective survival value of the modification of the thorax in such a nest-flea is apparent, particularly if it is faced with the problem of locating and attaching to its host in the dark, as in the case of bat-fleas and flying-squirrel fleas. However, fleas of volant and gliding hosts, or mammals living far above the level of the ground face a dilemma, because coupled with the need for restricted mobility there is the exacerbated problem of safely remaining attached to the host at such altitude (especially if it is volant). It is therefore not surprising that such fleas, lacking a pleural arch, have not followed the evolutionary path of fleas of underground nests and effected reduction of the combs, but instead, on the contrary, have developed supernumerary spines or combs. This is discussed below, in Sections C.3 and C.4.

The loss or reduction of the pleural arch and the resulting inability to jump well is also adaptive in other categories of fleas, e.g. the Antarctic flea *G. antarcticus*°. This flea lives in the nests of the silver-grey fulmar and the snow-petrel, amongst the rocks on the ground (for the former host) or in crevices (for the latter) (Murray et al., 1967). In the spring, the fulmar burrows to its former nest-site through the snow before it has melted, and the petrel also returns to its own individual nest-site. Incubation of eggs and rearing chicks takes 4 months, a period of warmth which is provided by the bird and which is obviously suitable, with respect to time and environment, for the life-cycle of the flea, because all stages have been found in the nest. An Antarctic flea of marine birds that was a good jumper could find itself in the sea, or exposed to extremely cold temperatures without a host. It is worth recalling that other fleas of marine birds have poorly developed pleural arches and are apparently poor jumpers

Of special interest are the hystrichopsyllids which seem to be nest-fleas by virtue of the reduction of the eye, thorax, and the number of bristles; loss of the pleural arch, etc. but which nevertheless have well developed ctenidia. In this group are insectivore-fleas like *Corypsylla*° (I.8) which possess a vertical comb near the frontal margin of the head which presumably hooks onto the hairs of the host as the flea abuts its head against the skin, as discussed by Traub (1968, 1969). The flattened frons and the vertical genal comb of the related *Stenischia*° suggest a similar habit. The question arises as to why such fleas, particularly *Corypsylla*°, whose ctenidia would seem to belie a true nest-existence, have lost the pleural arch and are such poor jumpers. In the first place, as is mentioned in Section IV.J below for *Corypsylla*°, and has been noted above in IV.B.2, for *Stenischia*°, there is reason to believe that such ctenidia are literally reduced as compared to those of relatives, and that they thus represent evolutionary tendencies shown by nest-fleas in general. Secondly, it may be that the peculiar vestiture of the head is an adaptation to stay affixed to the fur of a host while it is asleep in its home, and that these fleas are semi-sessile for hours and are indeed nest-fleas. In this connection, it should be noted

that the "banded" abdomen of these fleas, with its incrassate and rigid margins alternating with a softer middle, coupled with marked reduction of obtrusive abdominal combs and bristles, is ideally fitted to enable the insect to squeeze into, and out of, tiny cracks in the nest without being hurt, just as the reinforced segmental margins compensate for the loss of protection offered by the bristles of ordinary fleas. (It is significant that nest-fleas of birds are also "banded" but the alternating tanned and relatively soft sections of the abdomen extend from front to rear.) It therefore appears that these rhadinopsyllines are nest-fleas, at least in part, but there seems to be a third factor in the loss of the pleural arch, and that is the adaptive benefit to fleas which spend much of their time in narrow burrows, such as in the case of *Corypsylla*°, which infest moles and shrews. The question arises as to why such fleas have lost the pleural arch. It is, of course, possible for such fleas to utilize their specialized vestiture while feeding on a host that is in the nest asleep, and that development of this habit led to a semi-sessile existence and concomitant loss of the arch. However, other explanations for the *Corypsylla*-type of habitus seem more plausible. Fleas that jump well (e.g. *Ctenocephalides*) can leap heights of 8–10 inches (Traub, 1964), while moderately good jumpers like *X. cheopis* (Rothschild, 1903) may ascend to heights of 3–4 inches (Traub, 1964). Moreover, fleas usually make a series of leaps in succession. It is obvious that not only is there no need for such ability in fleas that may hatch out in, or frequent burrows that are only about $1\frac{1}{2}$ inches in height, but that the resulting forcible and repeated collision with the roof of the burrow could be disadvantageous to the species as well as to the individual. Shrews and other insectivores tend to establish runways above ground as well as below the surface, and limited ability to jump would restrict loose fleas to these particular sites, whereas otherwise they may end up in a micro-environment that is injurious or remote from any suitable host.

Support for this last-mentioned hypothesis is provided by a new species of *Stenischia*° from the Himalayas of W. Pakistan. Very few specimens of any of the other species of this genus are known, and hence their true hosts are in doubt. However, the Pakistani flea is a parasite of *Hyperacrius*, a small burrowing vole that only very rarely emerges from the underground. It seems logical that such a flea would be a poor jumper, just as it is not surprising that the *Palaeopsylla* of this mole-like vole bears ctenidia resembling those of *Palaeopsylla* of moles rather than those of shrews (Traub & Evans, 1967).

The presence or absence of a well developed pleural arch is also adaptive in the hypodermal, sticktight and semi-sessile fleas. Those, such as the pulicine *Echidnophaga* and *Spilopsyllus cuniculi* (Dale, 1878), which have to seek and infest an active, large host, and which are sessile only part of their lives, have well developed pleural arches, and are thereby fit for the vital "great leap forward" onto their host. The tungine burrowing and sessile forms, e.g. *Tunga*, in contrast, presumably have very little difficulty in finding and infesting their hosts at ground-level and remain affixed for life and have greatly reduced pleural arches. In the tungines, the evolutionary path has been towards suppression of the locomotory parts of the body (and even much of the limbs become resorbed after attachment or penetration), while the feeding and reproductive ends are hyperdeveloped. Marked reduction of

the entire thorax has therefore reduced the size of the target of the host bent on destroying the stationary flea and, in hypodermal species, has diminished the volume of body that must penetrate the skin of the host. In the case of *Echidnophaga*, etc., however, the advantage of being a good jumper outweighed the possible assets of loss of the pleural arch.

3. Hyperdevelopment of Combs in Bird-Fleas, Bat-Fleas, etc. Lacking the Pleural Arch. It has been stressed above that the loss of the pleural arch is apparently adaptive, whether in fleas of bats, birds, flying-squirrels, squirrels nesting in tall trees, or of hosts nesting underground or on the surface. It has also been noted that instead of showing a tendency towards the reduction of combs exhibited by fleas of underground nests, the fleas of bats, birds, flying-squirrels (and of nocturnal arboreal animals in general) display, on the contrary, a trend towards a significantly greater number of spines in the pronotal comb, and, in the bat-fleas, development of a series of true combs (vide fig. 98) or of false combs (Traub, 1968). These modifications likewise can be explained in terms of adaptations. As in the case of the bird-fleas in burrows on the faces of cliffs, and the squirrel-fleas in nests atop huge trees, bat-fleas face the hazards associated with heights, and substituting the facility to crawl and climb, for the ability to leap is advantageous to the individual and to the species. This is true especially in the case of eyeless bat-fleas and other fleas of nocturnal hosts, which would have less chance of locating their prey by a blind leap in the dark.

However, once on an active, agile, volant, gliding or leaping host, these fleas must solve the severe problem of maintaining their hold, regardless of whether the bird or mammal is perched, moving or trying to kill or remove them. A fall from such a height might not be fatal, or even injurious to a flea, but there would be little chance of finding a new and suitable volant or arboreal host on the ground, even if it were day-time and the flea could see. It is therefore to be expected that bird-fleas and bat-fleas have "supernumerary" spines in the pronotal comb as a result of natural selection (note figs. 89–91, and compare the bird-*Lentistivalius*, fig. 18 with the murid-one, fig. 16), and that many bat-fleas have fairly well-developed abdominal combs, or even ctenidia of false spines on the metathorax, or dorsal stiff, spine-like bristles forming a series of comb-like projections (Traub, 1968). Humphries (1966) independently came to the same conclusions about the adaptive value of the combs of bat-fleas. This same principle, it seems to me, also applies to the nest-fleas of arboreal squirrels, and this is why, although they lack the pleural arch, *Tarsopsylla*° (fig. 8), *Syngenopsyllus*° (fig. 3), *Libyastus*° (fig. 13) (all ceratophyllids) bear a full complement of spines, instead of having a reduced comb. Although precise data on the habits of some of these squirrel-fleas are lacking, the scarcity of records on the host and their demonstrated presence in nests lead me to believe that the last two are nest-fleas and/or infest nocturnal or crepuscular hosts, as mentioned below (p. 340). In the case of *Tarsopsylla*° (iii.1), Holland (1949), Smit (1953b) and Sakaguti & Jameson (1962) all cited it as a probable nest-flea, and its long, thin legs are also highly suggestive of a flea that crawls rather than leaps. It is noteworthy that the pronotal spines of these particular squirrel-fleas are somewhat narrower and relatively longer

than in the active fur-fleas of diurnal arboreal squirrels like some *Orchopeas* (figs 29, 31), *Opisodasys* (figs 46, 48) and *Monopsyllus* (figs 62, 64). This is presumably an additional step in the line of development, leading toward the adaptations of fleas of the flying-squirrels next discussed.

4. Hyperdevelopment of the Pronotal Comb in Flying-Squirrel Fleas, etc. As indicated above, the fleas of flying-squirrels tend to have a greater number of spines in the pronotal comb than do other members of the same genus which infest diurnal, arboreal squirrels or other hosts, and the spines are narrower and relatively longer, e.g. the Nearctic *Opisodasys* (iii.1) of flying-squirrels (fig. 47, *O. pseudarctomys*° and fig. 88, *O. vesperalis*°) versus *Opisodasys* from diurnal tree-squirrels (figs 44, 87, *O. hollandi* and fig. 48, *O. enoplus* (Rothschild, 1909)). The Bornean flying-squirrel flea, *Hollandipsylla neali*° Traub, 1953 (iii.1) also has a comb of this type (about 22 narrow spines). These particular flying-squirrel fleas also lack the pleural arch, unlike their allies, while in another (Himalayan) ceratophyllid of flying-squirrels, *Macrostylophora fimbriata* (Jordan & Rothschild, 1921) (fig. 97), the pleural arch is reduced as compared to allies on ground-squirrels, e.g. *M. borneensis* (fig. 96) and the pronotal comb likewise has a fuller complement than that seen in fleas of diurnal tree-squirrels (cf. fig. 7 versus fig. 14). A similar condition can be seen in comparing the ctenidium of a *Monopsyllus* from flying-squirrels (fig. 58) (iii.1) with one from ordinary tree-squirrels (figs 62, 64). The pleural arch of *M. argus* (Rothschild, 1908), from flying-squirrels, is also significantly shorter and narrower than in the *Monopsyllus* from tree-squirrels like *M. vison* (Baker, 1904). The Mexican *Orchopeas bolivari* Barrera, 1955 (New Combination) (iii.1) is believed to be a flea of flying-squirrels, and also shows this tendency (especially in the female), but to a lesser degree, perhaps because it is a recent association.

The same trend is seen in *Myoxopsylla*°, which are parasites of dormice, and although there are no known members of the genus occurring on other hosts which could be used for comparison, the comb extends more ventrad and has more spines than in related taxa, and the spines are also narrower. In *Monopsyllus sciurorum* (Schrank, 1803), which, despite its name, is a dormouse-flea, this same tendency is evident regarding a fuller comb and spines that are narrower in breadth and greater in number, as can be seen by comparing fig. 60 with the *Monopsyllus* of tree-squirrels shown in figs 62 and 64. It has been pointed out (Traub, 1969) that the fleas of nocturnal arboreal animals characteristically have a relatively large number of spines and that the comb descends sufficiently ventrad over the pronotum to reach or extend below the level of the third vinculum, while the lower spines are oblique in inclination, e.g. *Muesebeckella* Traub, 1969 (ii.1), *Acanthopsylla* Jordan & Rothschild, 1922 (ii.1), *Pleochaetis ponsi* Barrera, 1955 (iii.1), *Kohlsia keenani* Tipton & Mendez, 1961 (iii.1). *Tarsopsylla coloradensis*° (Baker, 1895) has a comb of this type, and from the figures cited, it can be seen that the comb of the *Opisodasys* of flying-squirrels and the other fleas of such crepuscular hosts approach this condition.

In the case of fleas of arboreal, nocturnal hosts, as with bat-fleas and fleas of nests atop tall trees, the pressures of natural selection would aid fleas that were crawlers, not good jumpers (hence the loss or reduction of the pleural arch), and/or which had

an elaborate pronotal comb that would help them latch onto and retain a hold on a gliding or highly active host operating in the night, usually at heights that would offer little chance of survival for a flea that was dislodged. It therefore is not surprising that the end-result in such fleas is a pronotal comb which superficially resembles that of bird-fleas because of "supernumerary" spines, but which differs in essential details as noted above and elsewhere (Traub, 1969).

Of special interest and relevance in this discussion is the remarkable monotypic genus *Scolopsyllus* Méndez, 1968, the only member of the family Rhopalopsyllidae having a pronotal comb. The enormously significant feature about this unique pronotal comb is that it consists wholly of false spines, paralleling the condition of the "false helmet" on the head of *Smitella* Traub, 1968. In these instances the spine-like structures arise from definite setal bases, instead of directly from the integument as in the case of true spines, and similar false combs have been noted as occurring on other parts of the body in other taxa (Traub, 1968). That author, writing before the discovery of *Scolopsyllus*, pointed out that such false combs function as regular ctenidia but suggested that they are *not* substitute mechanisms for true combs which have been lost in the course of evolution, since they occur on parts of the body which apparently have never borne true combs in the forebears of those particular taxa. Accordingly, he predicted that a rhopalopsyllid might be found with a well developed comb of modified bristles on the pronotum, and went on to state that "if a pronotal comb of specialized bristles were found to occur, it would be in a flea secondarily adapted to bank- or tree-nesting birds or else in a parasite of a nocturnal arboreal mammal." Now that a rhopalopsyllid has been discovered with such a ctenidium, it may be significant that the false comb extends down over the vinculum, analagous to the case of fleas known to infest arboreal nocturnal hosts as mentioned above. The true host of *Scolopsyllus* is not yet known, the seven existing specimens having been collected from three species of *Oryzomys* or from *Reithrodontomys mexicanus*. Méndez (1968) believed that "Factors related to the micro-habitat of the flea on the host-pelage rather than the habits of the rodent or climatological conditions, are perhaps responsible for such modifications." It seems to me, however, that the habits of the host account for the evolutionary development in *Scolopsyllus*, and that this comb is another instance of the adaptive mechanisms mentioned above as being typical in fleas having a special need for a device to help them fix on to a very active nocturnal or volant host.

The only fleas of arboreal squirrels which show a marked tendency towards a reduction in the number of spines in the pronotal comb, accompanied by an increase in their breadth, are those which are highly modified as true nest-fleas like some *Megarthroglossus*°, *Conorhinopsylla stanfordi*° Stewart, 1930 and *Epitedia faceta*. It seems significant that these are fleas of diurnal squirrels that nest in fairly short trees or else live in tree-holes near the ground surface. It may also be relevant that each of these genera include species which are nest-fleas of ground-dwelling Peromyscini. Hence the adaptation to squirrel-nests may be a secondaiy or later development. The nest-fleas like *Libyastus*° and *Syngenopsyllus*° which have a fuller complement of spines, as mentioned above, infest squirrels living in nests in very tall trees. Moreover, it may turn out that the true hosts of these little-known fleas are nocturnal

or crepuscular, especially in the case of *Syngenopsyllus*°. (It may be that *S. calceatus*° (Rothschild, 1905) is really a flea of flying-squirrels.) Regardless, the coupling of the comb of this type with the loss of the pleural arch is adaptive, as indicated. Similarly, even if *Tarsopsylla*° were a nest-flea of *Martes* (the fisher and martens) rather than of tree-squirrels, as records for at least the North American form suggest is possible, the argument is still valid, for the various species of *Martes* are nocturnal and largely arboreal. The possibility also exists that *Tarsopsylla*° is a nest-flea of flying-squirrels and if true, this would reinforce the above theories.

5. Convergence in Vestiture in Unrelated Fleas. That the above hypothesis about the evolutionary changes in the pronotal comb of fleas of flying-squirrels is correct is indicated by the modifications shown by the Australian *Choristopsylla tristis*°, one of the very few pygiopsyllids which lacks a pleural arch. Here we have the extraordinary case in which both parasite and host resemble, in important features, Nearctic species which are utterly distant phylogenetically and geographically. *C. tristis*° is a flea of *Petaurus*, a sugar-glider, a marsupial that looks and acts like a flying-squirrel (and, of course, there are no sciurids in the Australian–New Guinean area). Moreover, the flea exhibits reduced chaetotaxy, not only as compared with allied genera but also regarding *C. ochi* (Rothschild, 1904) (which has a very small pleural arch). The pronotal comb of *C. tristis*° bears about 10 narrow spines per side, resembling that of the ceratophyllid *Opisodasys vesperalis*° (fig. 88), a Nearctic nest-flea of flying-squirrels, but there are further and surprising parallels with nest-fleas of arboreal sciurids. For example, in *C. tristis*° there are 4 pairs of stout lateral plantar bristles on the last tarsal segment, with a mesal (ventral) pair in between the first pair and fully in line with them. (The mesal pair is in reality the true basal pair which has become displaced apicad and shifted towards the mid-line.) Thus, there is a total of 5 pairs of stout plantars in all. Ceratophyllids nearly always have 5 pairs of plantar bristles, and squirrel-fleas (and many others in the family) tend to have the first pair displaced somewhat mesad. However, the great majority of pygiopsyllids have 6 pairs, and the first pair is proximad of the second and only slightly moved toward the mid-line, e.g. *Acanthopsylla*. In *Bradiopsylla* Jordan & Rothschild, 1922, which is more closely related to *Choristopsylla* Jordan & Rothschild, 1922, there are only 5 pairs, but all are fully lateral. Even in *C. ochi*, which agrees with *C. tristis*° regarding displacement of the first pair, the third pair is somewhat shifted mesad, as in most members of the family, and there is also the customary dorsal pair of thin bristles on this segment, which *C. tristis*° lacks. *C. tristis*° is highly different from the general pygiopsyllids in another significant respect, and thereby also agrees with the *Opisodasys* of flying-squirrels in a trait that is highly unusual in the Ceratophyllidae—the first segment of the metatarsus is exceptionally long, being subequal to the tibia in length. In fact, the length of that segment approaches the condition in *Tarsopsylla*° (Holarctic squirrels or nests), which is almost unique in that the length of this segment I exceeds that of II–IV combined. (Liu & Li (1965) report that *Brevictenidia*, a monotypic genus of squirrel-fleas, resembles *Tarsopsylla*° in this respect.) Moreover, the relative length of metatarsus I in *C. tristis*° is significantly greater than that even in *C. ochi*, indicating specialization. The eye of the

former species is somewhat larger and better developed than in the latter (although still small), but it is equivalent to that of the *Opisodasys* of flying-squirrels (though ventrally excised instead of being entire).

Such parallels as those cited for the tarsi strain the credulity as being *bona fide* examples of convergence, but the precedent for such an extraordinary development exists in the Order, namely the shifting towards the mid-line of the third pair of plantar bristles of the apical tarsal segment, which occurs in 2 unrelated genera of bird-fleas, *Dasypsyllus* Baker, 1905 (iii.1) and *Ornithophaga* Mikulin, 1956 (iv.2) (Holland & Loshbaugh, 1958). Similarly, in the pygiopsyllid bird-flea, *Lentistivalius insolli*, the third pair of plantars is displaced to a greater degree than in the mammal-infesting species of the genus. The same tendency is seen in some other (not all) pygiopsyllid bird-fleas known to me.

An analogous shifting in the tarsal plantar bristles of bird-fleas has been noted earlier by Jordan amongst pulicids (1926) and cited as remarkable examples of convergence. In the tribe Spilopsyllini there are 3 genera (10 species) infesting mammals and all are combed, while 2 combless, monotypic genera parasitize sea-birds. In the mammal spilopsyllines the fifth tarsal segment bears 4 pairs of lateral plantar bristles of which the third pair is proximad of the middle or at the mid-line. However, in the bird-fleas, in *Ornithopsylla*, the third pair is shifted distad, whereas a similar trend is shown in the male of *Actenopsylla suavis* (shifted distad in mesotarsus and absent in the metatarsus) and the female has only 3 pairs on all legs. The case in the Xenopsyllini is more thought-provoking, for a similar development is seen only in the two *Xenopsylla* which occur on birds instead of rodents. *X. trispinus* Waterston, 1911 which infests *Petrochelidon* swallows in South Africa, is unique in that the third pair of lateral bristles on each side of segment is much nearer to the fourth pair than to the second. In *X. gratiosa* Jordan & Rothschild, 1923, a flea of *Puffinus*, a petrel, the third pair on the metatarsus gives the impression of being absent since one member is generally missing and the other displaced apicad and simulating a pre-apical plantar bristle (which are smaller and thinner than the laterals). On the other legs, in this species, both members of the third pair are shifted apicad and towards the mid-line. Thus, these bird-*Xenopsylla* exhibit a shift in the position of the third pair of tarsal bristles which Jordan (1926) alluded to as "crowding towards the apex," or else have eliminated these bristles. In all the mammal-*Xenopsylla* there are 4 pairs of lateral plantar bristles and the third pair is equidistant from the second and fourth. It is of interest that, as M. Rothschild & Clay (1952) have pointed out, the kittiwake flea, *Mioctenopsylla arctica* Rothschild, 1922 (iii.1) although a member of another family, also shows a tendency towards "a weakening and loss of tarsal bristles—at least in the hind-tarsus."

Holland & Loshbaugh (1958) in remarking on analogous tarsal modifications in *Ornithophaga* (iv.2) and *Dasypsyllus* (iii.1) state: "If this is a case of adaptive evolution it is surely a remarkable one, and the survival advantage of such a character is not apparent to the authors." My feelings are similar, but since we are now learning to appreciate that so many seemingly insignificant structural modifications of fleas do have meaning or function, perhaps the tarsal changes likewise do. However, Jordan (1926) offered another explanation for the tarsal modification in the bird-

pulicids. He pointed out that the "normal number of plantar bristles in Siphonaptera is 5 pairs; that is evidently the ancestral number, some genera having acquired more such bristles, many others having lost some of them." In the Spilopsyllini the trend has been to 4 pairs and hence "the tendency towards reduction already exists in the tribe." Jordan suggests that a "strong change in habit (or environment)" such as adaptation to birds as hosts "affects the growth and division of the chromosomes, rendering them unstable" and, in effect, this enhances the already existing genetic tendency towards modification of the plantar bristles. In short, the tarsal changes are unrelated side-effects that accompany the switch to a bird-host. Perhaps this is so, but certainly the many other modifications herein noted for bird-fleas and nest-fleas, etc. are apparently adaptive.

The fleas characteristic of *Aplodontia*, the sewellel or "mountain beaver" of the Pacific Coastal areas of North America, are instructive concerning several of the points that have been discussed, ranging from parallels in vestiture, to modifications suggestive of nest-fleas, shown by one species in particular. Three of the 4 *Aplodontia*-fleas: *Paratyphloceras oregonensis* Ewing, 1940, *Trichopsylloides oregonensis*° Ewing, 1938 and *Hystrichopsylla schefferi* Chapin, 1919, are hystrichopsyllids, and the first two belong to the Rhadinopsyllinae and the third is in the nominate subfamily. The fourth species, *Dolichopsyllus stylosus* (Baker, 1904) is a leptopsyllid in a unique monotypic tribe. In many respects the 4 species are as diverse as their generic names and taxonomic positions suggest, but they all agree in being very large, eyeless fleas, heavily clothed with a large number of very long, thin setae, and hence are remarkably similar in configuration (and thereby also resemble other fleas infesting burrowing mammals, as we have seen). The combed fleas of subterranean mammals like pocket-gophers and *Bathyergus* and *Aplodontia* (which not only digs well but spends most of its time in burrows) share another feature, and that is that the spines of the pronotal comb are unusually long and narrow, closely appressed and greater in number as compared to the condition in their relatives. The same tendency towards supernumerary, long, thin bristles and spines is seen in mole-fleas as compared to shrew-fleas, viz., the genus *Palaeopsylla* (Traub & Evans, 1967). It does not seem to have been noticed before, but there seems to be a definite correlation between the possession of a pronotal comb with many, narrow, close-fitting spines and chaetotaxy characterized by a plethora of long fine bristles. Thus, this is true not only for the fleas of burrowing hosts, but also for all the combed bird-fleas, their highly polyphyletic origin not withstanding. (As has been pointed out by Traub (1966) the trait of unusually fine setae is found not only in bird-fleas as compared to mammal-fleas, but also in Mallophaga, cimicid Hemiptera and hippoboscid Diptera which infest both kinds of hosts.) This suggests that the ctenidial and chaetotaxic modifications may be adaptive and are associated with the pelage of the hosts at the site of infestation. Moles, pocket-gophers, *Aplodontia*, etc. have very fine, dense fur, at least on much of their bodies and the pinnules of certain feathers are also delicate and it therefore seems likely that the vestiture of these fleas has been tailored by the processes of selection to fit that of their hosts, but direct or quantitative observations have not been made insofar as concerns these

particular fleas and animals. (Humphries (1966) in his fine paper on the function of combs, mentioned a bird-flea, but limited his studies to fur.)

In the case of the fleas of burrowing mammals there is another factor that merits further consideration concerning this condition of close-knit, lengthy fine hairs or spines which extend from one segment well onto the succeeding one. Such fleas infest hosts which are covered with earth and dust, and vestiture of this type must be useful in preventing such minute debris from slipping under the extensions of the terga and sterna. Fleas of other genera, when collected from mice covered with dirt in a trap, not infrequently have grains of soil imbedded under the overlapping segments. Many kinds of birds deliberately and frequently dust themselves in an action interpreted as aimed at reducing the itching caused by lice and other ectoparasites, and hence the same selective factor may be at work here in producing fleas with such modified vestiture. We lack sufficient data on the habits of birds and the infestation-rates of fleas to evaluate this hypothesis.

One of the *Aplodontia*-fleas, *Trichopsylloides*° has some of the characteristics of nest-fleas. Thus, it is essentially a *Rhadinopsylla*° which has lost its genal comb; and the pronotal comb does not extend down as far ventrad as in the other *Aplodontia*-fleas, and the spines are somewhat broader; there is no trace of a pleural arch; the legs are long and thin, etc. The only feature that suggests other habits is the chaetotaxy and the combination indicates that *Trichopsylloides*° is another instance of a nest-flea that can remain on the host when it leaves its nest.

6. Morphological Changes in the Thorax Associated with Lessened Jumping Ability in Fleas. In the Discussion thus far, reduced ability to jump has been shown to have adaptive value in many groups of fleas, ranging from bird-fleas and fleas of arboreal, nocturnal mammals, to fleas in nests underground. Methods of accomplishing this result are now considered.

Although the pleural arch has been reduced or lost in many instances and in a variety of taxa throughout the Order, a variety of mechanisms have been employed to achieve the conversion from a good jumper to a poor jumper or crawler, demonstrating that the term Convergent Evolution is an especially apt one in this case. In fact, the polyphyletic origin of the arch-less metathorax is apparent at a glance at figs 85–93, without recourse to the taxonomic characters used in systematics which placed the illustrated fleas in 5 families. This is not to say that representatives of each family modified the thorax in a manner that is characteristic of the family, for there are many variations on the thoracic theme in any one taxon (compare figs 85 and 86), and even in one genus there may be bewildering assortments (i.e. *Rhadinopsylla*). Fleas with a well developed pleural arch (PL.A.), and hence which are good jumpers, are shown in fig. 87 (*Opisodasys hollandi*) (iii.1) and fig. 91 (*Ceratophyllus styx*) (iii.1) and one with a fairly well developed one (*Xenopsylla vexabilis*) (ix.1) is illustrated in fig. 93. In such fleas, the resilin which provides the power-motif for the leap, is housed under the arch, above the apex of the pleural rod (PL.R.). Fleas lacking the pleural arch have no housing for resilin and hence are poor jumpers. Two members of the first two genera are in this category, and are illustrated in fig. 88 (*O. vesperalis*°) and fig. 90 (*C. arcuegens*°). *X. papuensis*° (fig. 92) has virtually no

pleural arch (PL.A.(?)) and no doubt likewise leaps poorly. These thoraces have been described earlier in the section on Data and Observations, along with that of a bat-flea (*Nycteridopsylla eusarca*°) which also completely lacks the pleural arch, and it will be recalled, and can be seen, that there are some significant differences in the metathorax of the 4 depicted species which are inferior jumpers. However, these variations pale in comparison with those of 2 hystrichopsyllid nest-fleas, *Conorhinopsylla stanford*° (i.2) (fig. 85) and *Wenzella obscura*° Traub, 1953 (i.8) (fig. 86) which also lack the pleural arch. In the former species, an anomiopsylline, the pleural rod (PL.R.) is very thin and elongate, extending dorsad of the level of the third vinculum (VC.3), and here joins the dorsal margin of the metepisternum (MTS.) as the latter continues dorsocaudad, beyond what is generally the anterodorsal limit of the metepimere (MTM.). (The tanned portion of the dorsal margin of MTM. in this species disappears just anterior to the spiracle.) A semi-membranous region which is the vestigial lateral metanotal area (L.M.(?)) is represented as the vertical, narrow, dorsal section of MTS., near the apex of VC.3. The rhadinopsylline *Wenzella*° is obviously built on an utterly different plan, as witness the large, downward projecting triangle of the metanotum (fig. 86, MTN.) which fits between the metepisternum (MTS.) and the metepimere (MTM.). The metepisternum (MTS.) is reduced and terminates below the third vinculum (VC.3); it is overlapped by the large mesepimere (MPM.), and is caudally flanked by the pleural rod for its entire height. There is no sign of a lateral metanotal area, and even the squamulum is undeveloped. The mesepisternum (MPS.) is unusually straight and angled along the anteroventral corner, and the phragma of the nota (PH.2 and PH.3) exceptionally pronounced.

The variety of paths used to reach the same end emphasize the adaptive nature of the response. However, sometimes the final products, superficially similar in appearance, may be achieved for different reasons, as shown by Johnson (1957), who presented an informative and interesting discussion of modifications of the lateral metanotal area, citing and illustrating additional examples than those just mentioned. She made the significant point that although *Pulex* and allied forms, are good jumpers, the lateral metanotal area has ventrally merged with the metepisternum, a condition which is also seen in poor jumpers like *Anomiopsyllus*°, etc. Johnson explained the paradox by stating that in the former "the metathorax has become heightened and narrowed" and indicating that "consolidation of the metepisternum and the lateral metanotal area would lead to greater strength" (for facilitating leaping). Moreover, *Pulex*, etc. possess a pleural arch. "In *Anomiopsyllus*° and allies (nest fleas and poor jumpers), on the other hand, the pleural arch is missing and there are few strong internal sclerotized rods left which might serve to strengthen the metathorax so far as jumping is concerned."

There is at least one other thoracic feature besides the loss or reduction of the pleural arch and the lateral metanotal area, etc., that is often associated with the lessened ability to jump and the concomitant facility of crawling into cracks and crevices, i.e., the reduction or loss of the chitinized dorsal margin of the metanotal flange (or diminution of this "collar"), along with the loss of the metanotal spinelets. This is seen in many swallow-fleas, viz., those which occupy nests used perennially (and not just for one season) and which hence are not faced with the problem of seeking a new

host elsewhere. The adaptive behaviour and physiological modifications of this first type of flea, which Darskaya (1959, 1964a) calls "settled" species, and of the "nomadic" fleas of the second category, will be discussed below (Section J). Here only the morphological features of the two types will be mentioned. In the "settled" group are the typical nest-fleas of the *C. arcuegens*° (fig. 90) and *C. delichoni*° pattern, which lack the pleural arch, but even those which retain the arch, are crawling, rather than jumping, species because the membranous or reduced metanotal flange permits a great deal of flexibility in the area of the junction of the thorax and abdomen, "while at the same time it deprives the flea's body of the fusion and compactness necessary for leaping" (Darskaya, 1959). Thus both *C. hirundinis* (Curtis, 1826), in which the metanotal flange is of this type, while the pleural arch is small and nearly contiguous with the top of the pleural rod, and *C. scopulorum* Holland, 1952, which has a fairly well developed pleural arch and a metanotal flange that is only somewhat modified, are adapted to crawl into crevices in the nest. In the typical nest-fleas particularly, but also in fleas like *C. hirundinis* etc., the caudal margins of the abdominal segments are more lightly tanned, permitting marked expansion of the abdomen when the flea engorges with blood prior to the long months of fasting when there is no bird in the nest, as is mentioned below. In contrast, fleas like *C. garei*, which have to leave their birthplace and seek out and/or leap on a host, have well developed pleural arches, "normal" metanota and are well tanned throughout.

Reduction of the posterior margin of the metanotum, including loss of apical spinelets occurs in some other bird-fleas, such as *Ornithophaga*, as noted by Holland and Loshbaugh (1958). This is presumably a flea of woodpecker-nests, or nests of tits, which also nest in tree-holes (Rosicky & Smit, 1965). The notable reduction in the number and girth of bristles; the narrow, feeble legs, the over-all light sclerotization, all suggest that the species of *Ornithophaga* are primarily "settled" or nest-fleas.

D. The Degree of Development of the Eye in Various Fleas

1. Comparative Size of the Eye. The degree of development of the eye of fleas varies tremendously amongst sundry groups of Siphonaptera, and sometimes even within a genus. Since some nest-fleas lack eyes, while in many they are reduced, and in some, are unusually large, it is necessary to discuss this topic before proceeding with subjects like the distribution of the nest-flea phenomenon in the Order.

It is well known that reduced or vestigial eyes occur in many unrelated fleas which parasitize subterranean or nocturnal hosts (Ioff, 1941; M. Rothschild & Clay, 1952; Traub, 1953; Traub & Barrera, 1966). Further, the allies of such modified fleas may have eyes that are much better developed, especially if they infest diurnal hosts. Amongst eyeless fleas of burrowing mammals are *Dactylopsylla* (iii.2) and *Foxella* Wagner, 1929 (iii.2), which infest Nearctic pocket gophers; *Pulex sinoculus* Traub, 1950 (ix.1), the only eyeless member of the genus and a parasite of Central American pocket gophers; (*Cryptoctenopsyllus*) *ingens* (i.4) a flea of the mole-like *Bathyergus*, which is essentially a blind and combless member of *Dinopsyllus* Jordan & Rothschild, 1913 (i.4) and hence its subgeneric status; and the monotypic *Cryptopsylla* (xi.2) which infests a South African bathyergid, (*Cryptomys*) with similar habits. Another such flea is the Angolan species for which C. Fox created the name *Rooseveltiella* in

1914, and which likewise parasitizes *Cryptomys*. Since this species is merely an eyeless *Xenopsylla* (ix.1), it is now called *X. georychi*. These hosts spend most of their life underground in dark burrows, and the eyes are minute in all of them. It is of interest that their fleas have followed a similar course of evolution. Although many species of *Ctenophthalmus* (i.3) have eyes that are only somewhat reduced, e.g. *C.* (*Ethioctenophthalmus*) *calceatus* Waterston, 1912, some species, such as *C.* (*Spalacoctenophthalmus*) *spalacis* Jordan & Rothschild, 1911, lack even a vestige. The latter is a flea of *Spalax*, a mole-rat whose eyes are so reduced that there isn't even an opening for the eye in the skin. The analogy continues with respect to hosts like moles (talpids) and burrowing voles (*Hyperacrius*), which spend much of their time underground—their fleas have greatly reduced eyes, as in the examples cited and illustrated by Traub & Evans (1967) and in *Hystrichopsylla talpae* (Curtis, 1826) (i.1), while burrow-frequenting or noctural animals like shrew-moles and shrews have small eyes, and again the condition is paralleled by their fleas, e.g. *Palaeopsylla* Wagner, 1903 (i.3), *Corrodopsylla* Wagner, 1929 (i.5) and *Doratopsylla* Jordan & Rothschild, 1912 (i.5), etc., in which the eyes are quite reduced. Nest-fleas of mammals which inhabit underground or enclosed nests (in hollow trees, etc.) and hence are in the dark virtually all the time, tend to have reduced or even vestigial eyes (figs 85, 86 and 92). Further, there is a direct correlation between the relative size of the eye of the flea and the amount of time the flea of underground nests spends on the host, away from its regular habitat. Thus, the less specialized neopsylline nest-fleas like *Epitedia* are not infrequently collected on the body of the rodent away from home, and in these fleas the eye is somewhat less reduced (fig. 98) than in the true nest-fleas (e.g. figs 85, 86, 92).

Mammal nests made of leaves and perched high in a tree probably admit more light than an underground one, but at any rate, squirrel-fleas like *Syngenopsyllus*° inhabiting such nests have eyes resembling those of flying-squirrels (fig. 97), i.e. somewhat smaller than those of diurnal fur-fleas like *Macrostylophora* (as in fig. 96) (which may live on diurnal squirrels residing in the same tree, or even the same nest, as *Syngenopsyllus*°).

Amongst nocturnal mammals with fleas with poorly developed eyes are bats in general; the New Guinean murines and marsupials infested with many genera of pygiopsyllids; rats in the Pacific Islands with *Sigmactenus* Traub, 1950 (iv.1) and *Neopsylla* (i.7), microtines with *Ctenophthalmus* (i.3) or *Amphipsylla* (iv.2), etc. However, some nocturnal or crepuscular animals have greatly enlarged eyes which enable them to utilize what little light may be available, e.g. lemurs, lorises, jerboas (*Allactaga*), flying-squirrels, etc. and it is of interest that a few fleas have developed along parallel lines, e.g. jerboa- fleas like *Mesopsylla* Dampf, 1910 (iv.2) and cricetid fleas like some *Ophthalmopsylla* Wagner & Ioff, 1926 (iv.2) (fig. 95), while some desert-*Xenopsylla* also have unusually large eyes (but others in the same habitat have very small ones) (Ioff, 1929; Traub, 1953). Mammals like flying-squirrels and dormice which are crepuscular or fairly nocturnal, and some species of rats with similar habits, have fleas with eyes that are well formed but small and oval (fig. 97). In contrast, fleas of diurnal mammals, such as squirrels, gophers, marmots, some

carnivores, pigs, etc. (except in the case of fleas specialized for living in underground or dark nests), have very large and well developed eyes (fig. 96).

It should be noted that virtually all known bird-fleas (other than the sticktight fleas, which have followed another evolutionary path) have relatively well developed eyes, whether specific nest-forms like *Ceratophyllus arcuegens*° (ii.1) (fig. 90) or a good jumper like *C. styx* (fig. 91). In fact, the eyes of fleas of terrestrial birds (whether ceratophyllids, leptopsyllids or pygiopsyllids) are generally characteristically larger than those of mammal-fleas, even if closely related. (This is one of the intriguing parallels that have accompanied this convergence to the bird-flea habitus, along with presence of many long and fine setae, etc.) All of these bird-fleas parasitize diurnal birds, however, and since the fur-fleas of diurnal mammals have well developed eyes, in contrast to the crepuscular and nocturnal forms, it is not surprising that the eye of the active types of bird-fleas is large. It is unfortunate that there does not seem to be any specific flea of a nocturnal bird, because it would be instructive to examine its eyes. However, the tendency for relative reduction of the once-hypertrophied eye does exist in nest-forms amongst bird-fleas. In *C. delichoni*°, the eye is rather small, symptomatic of "inhabitants of an ill-lit nest cavity" (Darskaya, 1959). The trend is also exhibited by some fleas of sea-birds which nest in burrows amongst rocks on the ground of small islands, and hence where the fleas presumably spend much time in the dark. For example, in *Actenopsylla suavis* (ix.1) the eye is quite small (fig. 99), more so than in related pulicids of terrestrial, diurnal mammals. The host of *Notiopsylla kerguelensis* (ii.1) also nests in such burrows, in the subantarctic (Smit, 1957), although the fleas also occur on the bodies of the birds, and it is worthy of note that the eye of this species is conspicuously smaller and more irregular than that of *Hoogstraalia* Traub, 1950, another pygiopsyllid, but one which infests the bodies of diurnal birds.

2. Vision in Fleas. It is obvious, then, that the size and degree of development of the eye in the fleas is associated with the amount of light in the environment in which the flea evolved. The corollary would seem to be that the ability of the eye to function is equally correlated with this light-factor. Thus, it would be expected that squirrel- and bird-fleas could "see" better than vole- or mole-fleas, but there seems to be little experimental data in this regard. Rothschild & Clay (1952) state that the eyes of fleas "are in fact displaced dorsal ocelli. These relatively simple organs probably do little more than enable their owners to perceive the difference between light and darkness and thus would only assist them in finding a host if it were in their immediate vicinity." Bates (1962) reported that sand-martin fleas (which have a well developed pleural arch) clustered about a burrow-opening on a cliff could hop onto a bird hovering by the aperture for just a few seconds. However, the stimuli causing this reaction are not known, nor has it been determined if the excited fleas merely leaped at random and just a few were successful in alighting on the bird.

Bates showed that these martin-fleas, over-wintering as adults in pupal cases inside old burrows occupied the previous year, emerged in the spring and moved towards the opening of the burrow and there remained motionless, in clusters, with the heads pointing towards the aperture. It seems likely that the movement

towards the opening, where the fleas would be in a position to leap onto a returning migrant that hovered by the hole, is a response to light, but this is not definitely known. However, these fleas were also shown to possess the ability to disperse from old burrows and emigrate as much as 33 meters and enter new burrows. While entrances to new burrows apparently were not detected by vision, the means to do so could not be determined, although it was learned that the fleas somehow recognize horizontal floors of burrows (as distinguished from the flat top of the bank) and tend to congregate there.

M. Rothschild (1969) reported that many fleas are negatively phototropic and jump away from a bright source of light (and the ones that she mentioned have relatively well developed eyes). Such fleas would generally move towards the shade, if given a choice between light intensities, but a few individuals would move *towards* the light.

Humphries has rendered a great service studying in detail such long neglected subjects as the behaviour of fleas, and among his important contributions are observations on *Ceratophyllus gallinae* (Schrank, 1803), the hen-flea (1968). Humphries noted that *C. gallinae*, after emerging as adults in the nest, are generally negatively phototropic for about 2 days, and as a result, stay in the nest rather than dispersing before mating. (The nests usually remain deserted by the hosts unless they return within that period.) Thereafter, the fleas exhibit a positive phototaxis and negative geotaxis, leave the nest and move upwards on the tree harbouring the nest. During the ascent, the fleas frequently pause for long periods and then resume climbing upwards if a host is not encountered. When in the immobile phase which Humphries termed a "stance", the fleas would immediately leap towards a small object that suddenly reduced the intensity of light. Humphries concluded that these responses were connected with locating a host and showed that fleas would readily leap upon an object the size of a small bird which moved about and paused on the branches. If, upon leaping, the *C. gallinae* missed Humphries' imitation-bird, they would alight on the ground and then climb up on the vegetation and start anew. As a result, even if they were only on grass, they would be in a position to leap upon a ground-bird casting a shadow.

Thus, while we really do not yet know how well fleas can see, it is apparent that they do respond to light and that those with eyes tend at times to move definitely or precipitously towards shadows. It therefore seems that regardless of other existing stimuli (vibrations, odor, carbon-dioxide, etc.), the sudden appearance of a host by the nest or by the burrow-aperture would cause a distinct change in light-intensity that would attract or spur fleas to leap upon their hosts. Contrariwise, such a shadow could not be thrown in a dark burrow underground, where the fleas lack the eyes to appreciate such changes anyhow. Darskaya (1954a) noted that *Citellophilus tesquorum* (iii.1) (which has well developed eyes) often cluster in great numbers about the burrow-opening of the suslik, *Citellus dauricus* (which is active during the day) and readily infest any ground-squirrel that puts its head in the hole or lingers nearby.

The facts that fur-fleas of diurnal, large mammals have well developed eyes, e.g. *Pulex* Linnaeus, 1758 (ix.1), *Ctenocephalides* (ix.1), *Pariodontis* Jordan & Rothschild, 1908 (ix.1), *Paraceras* (iii.1), *Oropsylla* Wagner & Ioff, 1926 (iii.1), *Thrassis*

Jordan, 1933 (iii.1), *Opisocrostis* Jordan, 1933 (iii.1), sundry vermipsyllids (x), infesting man, pigs, some carnivores, Old World porcupines, badgers, marmots, or prairie dogs, etc., and that these all seem to be excellent jumpers, lead me to believe that the large eye is of use to these fleas in finding their hosts.

The fleas of the small rodents which are diurnal, likewise have well developed eyes (unless, of course, they are nest-forms) and the same line of reasoning applies regarding the function of such eyes is further supported by Darskaya's detailed and well executed studies on *X. gerbilli caspica* and its desert-host, the gerbilline *Rhombomys* (1955). She states the "daily activity of these fleas is to a certain degree tied to the regime of light and daily activities of their hosts." It is of interest that Darskaya reported that *X. g. caspica* (which has a fairly well developed eye) will cluster at the mouth of the *Rhombomys* burrows, particularly if they had hatched out in a burrow-system that was no longer occupied (1955). Such hungry fleas have been known to instantly attack virtually any mammal near the opening and have been noted to follow such prospective prey for at least 2·5 meters. If they fail in their efforts to alight on the animal, they attempt to return to the burrow-openings.

The association between the size of the eye of the flea and the degree of development and utilization of vision in the host is so profound, that I was long disturbed over the eyeless condition in *X. papuensis*°, for I know of no truly burrowing mammals in New Guinea, and existing records were from *Pogonomys*, a somewhat scansorial rat. However, after collecting some of these fleas in *underground* nests of *Pogonomys* on several occasions, it became clear that this species was merely exhibiting the same trend noted in other nest-fleas elsewhere, even to the extreme reduction of the pleural arch.

In general, fleas possessing a *genal* ctenidium have a reduced eye, and the few exceptions are clearly adaptive. Thus, *Hoogstraalia* (ii.1) has a well developed genal comb and a large eye but it is a bird-flea, and as we have seen, an eye of that type is characteristic of such fleas. *Ctenocephalides* (ix.1) is similarly adorned, and since these fleas may hatch out anywhere in the haunts of the host, as indicated below, they may have to seek out and infest their hosts (large mammals) during daylight. As originally noted by Karl Jordan (1950) and discussed by Traub (1969), in fleas in which there is an evolutionary trend towards assumption of a vertical comb on the head, the vestigial eye is progressively displaced dorsad as the number of spines in the comb increases (e.g. *Peromyscopsylla*, *Leptopsylla* Jordan & Rothschild, 1911, *Sigmactenus*, etc.), indicating that the head-ctenidium in most cases is genal in nature (unlike the in helmet-fleas and in *Smitella* Traub, 1968 (ii.1)).

3. The Types of Thorax in Fleas with Reduced Eyes. Inasmuch as many characteristic fleas of bird-nests have well developed eyes but lack the pleural arch, while many mammal-nest fleas with such a thorax have very small or vestigial eyes, it is clear that reduction of the eye has proceeded independently of loss of the pleural arch, the former associated with the amount of light in the environment, the latter with lessening of the ability to jump. The two phenomena often coincide because conditions under which the environment is invariably in darkness are frequently those in which reduction in jumping-ability is also a useful attribute. Examples

have been cited in which the eye is large but the pleural arch is missing (e.g. many bird-fleas and nest-fleas of diurnal arboreal squirrels). In many species besides true nest-fleas the eye is so reduced as to be indistinct, and this topic merits consideration with respect to (1) species in which the pleural arch is present, and (2) species lacking the pleural arch but simultaneously showing adaptations for remaining on the fur of the host. In the first category are fleas of mammals like shrews, voles and other hosts that are primarily nocturnal and/or spend much time in burrows, but in which the fleas are adapted for attachment to pelage by means of combs of spines, dense or plural rows of bristles, or false combs of modified bristles. Examples like *Doratopsylla* (i.5) have already been cited. Here also belong other hystrichopsyllids such as *Neopsylla* (i.7), *Rothschildiana* (i.7), *Stenoponia* Jordan & Rothschild, 1911 (i.9), *Hystrichopsylla* Taschenberg, 1880 (i.1), etc., as well as leptopsyllids like *Peromyscopsylla* (iv.1), *Acropsylla* Rothschild, 1911 (iv.2), *Paractenopsyllus* Wagner, 1938 (iv.1), etc. and many chimaeropsyllids (xi.). It is noteworthy that eyes of this type are apparently unreported in ceratophyllids, although the more "degenerate" condition of virtual total absence occurs in the pocket-gopher fleas, which are members of this family. The condition of a reduced eye is approached, however, in *Malaraeus* Jordan, 1933 (iii.1) which is the name ascribed to a polyphyletic and somewhat anomalous assemblage of fleas characterized by the common character of a small but oval eye. Certain *Jellisonia* (iii.1) and *Kohlsia* (iii.1) also have an eye of this type. Very few pygiopsyllids have a well developed eye, but in most species the eye is fairly large and well pigmented, although ventrally excised. In the South American and Central American genus *Ctenidiosomus* Jordan, 1931 (ii.1), however, the eye is reduced and fragmentary, and the species have multiple combs of spines. In the second group, "blind" fleas which lack the pleural arch but which bear special or well developed pronotal or even genal combs, or are otherwise modified for host-attachment, are the insectivore-fleas like *Corypsylla* discussed in Section IV. C.2 above.

E. The Evolution of the Characteristic Pronotal Comb Ascribed to most Nest-Fleas

It has been shown above that throughout the Order, a variety of fleas have developed the habit of feeding on their hosts while the latter are in the nests, and have become modified accordingly. A wide assortment of hosts are involved, and their habits have affected the path of development of the adaptive responses of the fleas, as host and parasite evolved together in close association. As we have seen, the pronotal comb of nest-fleas infesting aerial hosts (bats and birds) (figs 89, 18, 90, 91) or those that parasitize arboreal, nocturnal hosts (figs 47, 88) tend to have an unusually large number of spines in the pronotal comb, as compared to allied taxa (figs 17, 46). However, nest-fleas of hosts nesting below ground or at, or near, the surface, tend to have pronotal combs in which there are fewer spines than "normal" and the spines are frequently short and broad (figs 67–84), and as previously indicated, such convergence cannot be ascribed to parallel proclivities in pelage. Instead, it seems that the pattern of the pronotal comb exhibited by fleas of this last category can only represent evolutionary stages in the general reduction of spines and bristles so characteristic of these nest-fleas, and which accompany such "modifications by reduction or loss"

as has been noted for the eye, pleural arch, metanotum, size of metepimere, girth of legs, etc.

Examples have been cited above repeatedly showing how nest-fleas have lost or reduced these structures or a combination thereof, in approaching the configuration of the virtually nude species of *Anomiopsyllus*° and the combless, eyeless, slender *Wenzella*°. That reduction in the number of spines in the combs has accompanied the loss of bristles is not only indicated by the general trend, but by the fact that the genera with the fewest, and stoutest spines, e.g. *Megarthroglossus*° (i.2) (fig. 75) and *Conorhinopsylla*° (i.2) (figs 73, 86) are those with the most marked loss of setae. The setae seem to become narrower as they approach extinction in the course of evolution, but in the case of the pronotum the spines frequently become shorter and broader as in the nest-fleas. *Phalacropsylla* (i.7) approaches the last two genera with respect to the points mentioned. *Brachyctenonotus*° (iv.2) has a comb of extremely short spines, but these are fairly broad and the comb is almost full length (in height). *Calceopsylla*° (iv.2) duplicates the condition in *Brachyctenonotus*° regarding tiny spines, but the spines may be somewhat more slender and the comb is not quite as short. The pronotal ctenidium in many of these nest-fleas extends ventrad to near the vinculum, but it is definitely shortened in *Rhadinopsylla* (i.8) (fig. 72) and most neopsyllines (i.7) (figs 67, 70, 78, 76). In other instances, impending loss of the comb is indicated by the reduction in the vertical extent of the comb and in shortening of the spines, as in the chimaeropsyllids and in *Agastopsylla*° (i.3), or by loss of pigmentation accompanying reduction in length, as in *Mioctenopsylla* Rothschild, 1922 (iii.1) and *Brevictenidia* (iii.1), or as in both genal and pronotal combs in *Agastopsylla*. The loss of abdominal ctenidia by marked reduction of the number and size of the spines and by the shortening of the height of the comb as has been discussed by Traub & Evans (1967) and is also illustrated in the bat-flea *Nycteridopsylla eusarca* (v.1) (fig. 89).

A different mechanism for the loss of pronotal spines can be seen in *Corypsylla ornata*° (i.8) (which may not be a true nest-flea in that it is simultaneously adapted to remain on the host) and involves sexual dimorphism. Here the male has a full length comb of spines, of which the upper fourth are long and stiletto-like, and the emainder becoming progressively shorter and less acutely pointed. The shortening in length is accomplished mainly by the loss of the base of the spines, and not merely by abbreviation of the apices; the proximal ends of the spines forming a sigmoid line whose lower $\frac{2}{3}$ is markedly convex. The original full length of the spines is indicated by pale outlines and caniculi. In the female, however, the dorsal $\frac{3}{5}$ of the comb consists of stiletto-like spines, which also become progressively smaller, but the lower $\frac{2}{5}$ of the comb is represented only by pale blunt nubbins of spines which are more like denticles, with long caniculi proceeding to the former base of the comb.

The two known genera of malacopsyllids (xiv) (both monotypic) are not nest-fleas, although they have followed another path leading toward reduction and loss of combs, namely the development of the "sticktight" habit. It is instructive that *Malacopsylla* Weyenbergh, 1881 has no ctenidia at all, but that in *Phthiropsylla* Wagner, 1939, the pronotal comb is represented by but 3 very short, broad spines or "teeth" which are widely spaced.

The tendency towards loss of ctenidia is general throughout nest-fleas in the Order, as shown by the fact that combless members amongst such fleas occur in 5 of the families which include nest-species, while the trend is also demonstrated in the sixth (Leptopsyllidae). There can be little doubt that intermediate steps in the evolutionary path, and not the structural peculiarity of the pelage, account for the convergence of patterns of pronotal combs seen in these nest-fleas inhabiting underground nests, etc.

F. Distribution of the Nest-Flea Phenomenon in Siphonaptera

Although nest-fleas occur throughout the Order, it is apparent from what has been written above, that the phenomenon is much more common in certain groups of fleas than in others, and that the degree of specialization exhibited varies considerably. Both of these points can presumably be explained by the following factors: (1) The duration and extent of the association between the fleas and their respective hosts. (2) The phylogeny of the fleas and of their hosts. (3) The ecology of the area concerned. (4) The habits of the host. (5) The habits of the fleas. The relative geological ages of the various groups of fleas and some of their hosts will be treated at some length in a subsequent article (Traub, in preparation) but a brief discussion of certain elements is warranted at this time, while considering the other points.

The vast majority of the nest-fleas are members of the Hystrichopsyllidae (referred to as family i), where representatives occur in 4 of the subfamilies. There were several examples cited for the Ceratophyllidae (iii), but relatively few for the Pulicidae (ix) and Leptopsyllidae (iv). The proportion of nest-fleas is fairly high in the Chimaeropsyllidae (xi) but the family is a small one and only a few species are actually involved. The condition is rare amongst known Pygiopsyllidae (ii) but the dearth may be more apparent than real, for the following reasons. (1) The family is primarily Australian–New Guinean in distribution, with relatively few species occurring in the Asiatic–Pacific islands, the Indo–Malayan region and Central Africa. Throughout much of their range therefore, the pygiopsyllids are found in regions of heavy rainfall and hence where mammals make few underground nests because of the high water-table and flooding, and where relatively dry, hollow cavities in logs, stumps and trees are rare or absent. In such an environment there has been little opportunity for development of the nest-habit in fleas, except perhaps for those infesting arboreal hosts living in tree-holes or making some sort of aerial nest that adequately sheds water. (2) Relatively few mammal-nests have been examined for fleas throughout the entire range of the pygiopsyllids, and even the fur-fleas of indigenous Australian rodents and marsupials are inadequately known. The same is true for body-fleas in the other areas, save New Guinea. It seems likely that pygiopsyllid nest-fleas await discovery, perhaps in xeric areas of Australia or in arboreal species elsewhere.

Very little has been written about the phylogeny of the various families and other groups of fleas (Traub, 1968), and it is beyond the scope of this article to do more than point out that the families Hystrichopsyllidae and Pygiopsyllidae are regarded by me as being ancient and primitive in many respects (but specialized in others), while the Pulicidae is considered to be a very old, but yet more advanced family than

the first two, and the Leptopsyllidae, Ischnopsyllidae and Ceratophyllidae are deemed younger. Reasons for these views are cited in another article (Traub, in preparation), but are based on three considerations: (1) Morphology, including general skeletal structure and comparative anatomy of the aedeagus. (2) Host-relationships. In general, the more primitive and oldest fleas are associated with the more primitive hosts, and the more specialized fleas with the more advanced (and younger) mammals. (3) Zoogeography. Fleas essentially restricted to two or three of the southern continents are believed to have spread amongst those areas when island-hopping links still existed between them, well before Australia and South America became isolated.

In general, the hystrichopsyllids infest mainly insectivores, cricetids, and sciurids, while the ceratophyllids, on the whole, parasitize mainly cricetids and sciurids, and some murids. Relatively few hystichopsyllids (e.g. some *Neopsylla*) and ceratophyllids (e.g. certain *Nosopsyllus*) infest the genus *Rattus* and it is significant that there are no known nest-fleas specifically associated with *Rattus*, which is believed to be a recently evolved group. Leptopsyllids are rarely specific to insectivores except perhaps for tenrecids in Madagascar, and instead are found on murids and, particularly in the Old World, on cricetids. Some leptopsyllids are associated with dipodids and gerbillines and a few with ground-dwelling Palaearctic sciurids and lagomorphs. The pygiopsyllids are, on the whole, either fleas of marsupials or murids. Pulicids are found to parasitize a broad range of hosts when considered as a family, but some specialization is shown by certain of the subgroups. Many are sticktight fleas or "burrowing" species like *Tunga*, as has been indicated, and these need not be considered further. The spilopsyllines include rabbit-fleas which tend toward semi-sessile habits, and the two genera of nest-fleas of marine birds treated elsewhere. The xenopsyllines are primarily fleas of gerbillines (and hence occur in rather xeric areas) or are mane-fleas. The archurieopsyllines include carnivore-fleas like *Ctenocephalides*, hedgehog-fleas, and one odd rabbit-flea, a Madagascar tenrec-flea and the African *Aphropsylla*, whose true hosts are unknown.

The questions arise as to why the bulk of the nest-fleas occur in the hystrichopsyllids, why the phenomenon exists in so many subfamilies and tribes thereof (e.g. 7 of 8 Anomiopsyllinae genera and 8 of 11 genera of Neopsyllinae), and why the examples include some of the most highly specialized nest-fleas, e.g. *Anomiopsyllus*° and *Wenzella*°. Inasmuch as the host-associations and morphology of the hystrichopsyllids suggest that the family is an ancient one, the obvious answer is that hystrichopsyllids and their hosts have been associated intimately for eons, long enough for the nest-habit of fleas to have evolved and progressed to the point of extreme specialization by reduction. Nevertheless, it must be pointed out that, for unknown reasons, very few instances of the relationship involve insectivores, which are believed to be low on the phylogenetic scale. Virtually the only examples are some species of *Rhadinopsylla*, and these are not highly specialized, and may not be specific. Perhaps if more were known about the fleas of nests and shrews in North America and northern South America, some such true nest-fleas would be discovered, but it may be that the nests of shrews are too transient for such fleas to have evolved, and this is why virtually all shrew- and mole-fleas are adapted for remaining on the host. Regardless, hystrichopsyllids are found on all continents, but have an extremely discon-

tinuous distribution, e.g. huge gaps over most of South America, and known endemicity in a restricted portion of Australia, with the geographically closest members of the family occurring in Borneo and Indonesia. Such a range also bespeaks of antiquity, as does the existence of two endemic subfamilies in Africa. Nest-fleas occur in virtually all of these areas, perhaps also including Australia. The highly modified *Anomiopsyllus*° and *Wenzella*° are parasites of heteromyids, a group that arose in the early Oligocene, with some modern genera occurring at least in the Miocene (Simpson, 1945). A large proportion of these hystrichopsyllid nest-fleas (e.g. *Megarthroglossus*°, *Stenistomera*°, *Callistopsyllus*°, etc.) are (like *Anomiopsyllus*°) associated with the fauna of the deserts of North America, another phenomenon that was Oligocene in origin. For these reasons, the extreme age of the family and its associations seem to have been an important factor in the evolution of the nest-habit.

The sciurids and leporids, however, are older than the rodents mentioned above, and yet the family of fleas most closely connected with squirrels, the ceratophyllids, include only a few nest-fleas. Here we must differentiate between the geologic age of a group of mammals and the duration of the association of the fleas with such animals, for they may be very different. For example, although birds arose far back in geological time, their parasitism by fleas must be relatively recent, for the sundry bird-fleas, representing several different families, are all supposed to be derived from mammal-fleas (Rothschild & Clay, 1952; Holland, 1964; Traub & Barrera, 1966). That this was so, was well known to Jordan (1937) and N. C. Rothschild (1917), and Ioff (1928) also referred to this phenomenon in pointing out that bird-fleas of the *Ceratophyllus gallinae* group are related to mammal-fleas now referred to as *Monopsyllus*, e.g. *M. sciurorum* and *M. tamias* (Wagner, 1927). Ioff further noted the close affinities of the rodent-infesting *Frontopsylla* with those on birds (but which are today called *Orfrontia* Ioff, 1946). Moreover, the bird-infesting genus *Ceratophyllus* itself is believed to be of polyphyletic origin. Another point is that the particular genus, tribe or subfamily of host may be relatively recent in origin even though the stock is ancient. One feature that is quite striking is that there *are* quite a few nest-fleas parasitizing sciurids, but most of these not only are hystrichopsyllids, e.g. *Conorhinopsylla*°, *Megarthroglossus*°, *Rhadinopsylla*°, *Epitedia*, *Tamiophila*, etc., but genera which also includes species which are nest-fleas of peromyscines and other cricetids, and hence may represent recent transfers to sciurids. Actually, true squirrels are known from the Miocene, while the groups of tree-squirrels may be much younger, but the fossil record is scanty (Simpson, 1945). It may very well be the relative youth of the tree-squirrels that accounts for the comparatively small number of nest-fleas known amongst such hosts, and for the low degree of specialization shown by such ceratophyllids, despite the selective pressure exerted, for such an evolution, by the hazards of existence encountered by fleas in the high trees. It is noteworthy, however, that the bulk of the ceratophyllid nest-fleas of mammals is found amongst the parasites of squirrels nesting in high trees or amongst flying-squirrels. Another factor for the apparent dearth of nest-fleas in this family is the presumed modernity of ceratophyllids as compared to the hystrichopsyllids—there hasn't yet been time for the marked reduction in head, thorax, etc. to occur.

Offhand it seems strange that so few nest-fleas are known to parasitize the Marmotini, the tribe including the northern ground-squirrels (*Citellus*, etc.), marmots (*Marmota*), prairie-dogs (*Cynomys*), chipmunks (*Tamias*, etc.), and which is believed to have arisen in the Miocene (although all records save for *Citellus* are Pliocene or later). A wealth of genera and species of ceratophyllid fleas such as *Citellophilus* Wagner, 1934, *Callopsylla* Wagner, 1934, *Thrassis*, *Opisocrostis*, *Oropsylla*, *Diamanus* Jordan, 1933, are associated with these rodents that essentially are ground-squirrels but which vary in size from small to huge, but only the occasional species like *Callopsylla dolabris* (fig. 84) seem to be developing the nest-habit. (It should be noted that the fur-fleas of *Citellus* and other true ground-squirrels, such as *Citellophilus*, *Opisocrostis*, *Thrassis* and *Diamanus*, do not exhibit the tendency towards broadened subventral pronotal spines of the fleas of the arboreal and semi-arboreal squirrels.) The other nest-fleas occasionally encountered on chipmunks and *Citellus*, etc., are hystrichopsyllids, e.g., *Tamiophila*, as has been pointed out to be the case for the nest-fleas of tree-squirrels. The marmotines burrow and nest underground in habitats that should favour the production of nest-fleas, for they abound with other types of fleas, some of which have long palpi (like *Diamanus*, etc.), indicating feeding at leisure. One contributory factor may be that these hosts are all diurnal, meaning that any flea which lingered on the host would be exposed to light considerably, especially if it fell off—or developed from an egg that had been hatched out on the ground surface. Fleas with reduced eyes would be at a selective disadvantage under such conditions, and it is reiterated that virtually all of the nest-fleas of mammals have hosts that are crepuscular or nocturnal.

Many, if not most, of the ceratophyllids of burrowing rodents are well known for swarming about the opening of the burrow (Darskaya, 1954a, 1955), and this habit no doubt is all associated with the presence of a well-developed eye. In this way, the fleas are able to leap upon rodents that approach or enter the burrow, or even pursue them for a while (Darskaya, 1955). In all probability, these fleas have hatched out in the nest or in various depths of the burrow and move toward the light source at the aperture, as Bates (1962) observed for the perambulatory type of sand-martin flea. Thus, the evolutionary trend of the ceratophyllids has in general been in directions opposed to the formation of true nest-fleas, although the time factor of length of association between host and flea may also be important.

Leptopsyllids on the whole have followed much of the route of the ceratophyllids insofar as concerns evolution of habits of infestation, but have detoured with respect to host-range and have become delayed regarding distance traveled. Thus, very few genera and species occur in North America (where all native forms except two are associated with lagomorphs), whereas the ceratophyllids are the dominant members of the Siphonapteran fauna in that part of the world. Leptopsyllids not only infest cricetids but to a great extent parasitize murines, one species having even accompanied *Rattus* to New Guinea, whereas there are no native murids in the New World. (The last-mentioned point no doubt helps account for the dearth of leptopsyllids in North America.) There has been little association of leptopsyllids with sciurids and virtually none with tree-squirrels in particular. Except for fleas of murines (which are nocturnal), nearly all leptopsyllids have fairly well developed eyes, while the

bird-infesting species have large eyes. In general, they seem to be good jumpers and rodent-species may be common around burrow apertures, while nearly all are modified for remaining on the body of the host. The few known species that seem to be nest-forms have converged along the familiar lines indicated above. One relevant and possibly important factor in this discussion is that there still is a great deal to be learned about the nest-inhabitants of desert rodents throughout much of Asia (excluding well studied areas of the U.S.S.R.). The majority of North American nest-fleas are found in xeric areas, and very few leptopsyllids are represented in the fauna, whereas members of this family are common and wide-spread in the Asian counterpart terrain. The African nest-fleas are also inhabitants of deserts and semi-deserts, in the main. The equivalent fauna in Asia may therefore be better developed than current data indicate.

The answer to the question as to why nest-fleas are poorly represented amongst pulicids lies in the evolutionary sequences observed in that family, viz., development of sticktight fleas or else active species with well developed eyes, which are good jumpers and which are so highly adapted that they can feed and thrive on an exceptionally broad variety of hosts. It should be noted that just because a flea has sticktight habits, it does not mean that it is *ipso facto* a poor jumper, for the behaviour of a flea after it finds and attaches to its host may be quite different than it was beforehand. Some sticktight fleas like *Echidnophaga* Olliff, 1886 (ix.1), which are essentially sessile after attaching, are excellent jumpers. Thus, *E. gallinacea* (Westwood, 1875) can leap 200 times its own length (M. Rothschild, 1969), a fact that is useful when it encounters its usual prey of medium or large size, such as rabbits, carnivores, pigs, chickens, etc.

The catholicity of pulicids regarding hosts is illustrated by the so-called cat-flea *Ctenocephalides felis* (Bouché, 1835) which has not only been collected in numbers on all sorts of carnivores, including dogs, foxes, wolves, jackals, tigers, *Felis bengalensis* and other "wild cats," racoons, coati-mundi, weasels, mongoose and other civets like the binturong (*Arctictis binturong*), but on man, opposum, cattle, horses, sundry rodents, lagomorphs, hedgehogs, bats and the armadillo, etc. (Traub, 1950; Hopkins & Rothschild, 1953; Hoogstraal & Traub, 1963a, b, 1966; and unpublished data). It has also been known to feed on lizards (Fox, Fox & Bayona, 1966) and the related *C. canis* (Curtis, 1826) has been reported sucking blood from a lizard (Jäth, 1952). There are not many records of *C. felis* from rodents, as compared to the large mammals, but this, I believe, reflects its superior ability as a jumper, and not to any inherent predilection or aversion, since it ordinarily vaults too high to strike a rat-sized animal. The plague flea, *X. cheopis* is notorious for feeding on man as well as rats, but has a very broad host-range in general, from a variety of murines and other rodents, to shrews, lagomorphs and bats, as cited by the sources mentioned above. In this case, the vast majority of records are from small hosts, for *X. cheopis* does not leap as high as *Ctenocephalides*. *X. gerbilli caspica* has been reported to feed on lizards (Darskaya & Besedina, 1961; Kulakova, 1964).

The majority of the pulicids are compact, i.e. relatively short and broad, a type of build that is often seen in fleas that are good jumpers. The species, whose life-histories are known, tend to lay eggs loosely among the hairs of the host, as in *Cteno-*

cephalides, so that the larvae and adults are apt to emerge in the haunts of the host, rather than in the nest. Larvae of the desert-species *X. conformis* (Wagner, 1903) have been found to be abundant in the rodent-burrow, at the entrance, indicating that the eggs can develop wherever they fall, if conditions are favourable (Darskaya et al., 1962). In the case of large mammals (e.g. *Pulex* and pigs) this can be almost anywhere. This particular trait of egg-laying is associated with fleas with large eyes and a well developed pleural arch, as has been noted. For these reasons, development of the nest-habit in the Pulicidae has occurred only under special circumstances, as in some of the fleas associated with burrows of marine birds and in underground nests of *Pogonomys*, etc. A few *Xenopsylla* associated with the desert have small eyes, as befitting ectoparasites of nocturnal hosts that wouldn't emerge from their burrows during the heat of the day.

The evolution of the nest-habit virtually by definition is limited to fleas of hosts that (1) have a specific nest or burrow and (2) reside there continuously or else return to live or breed there the following year or season. It is probably for this reason that no true nest-fleas are known amongst the rabbits and hares (leporids), and that instead, the rabbit-fleas often act somewhat like sticktight species. It is noteworthy that the rabbit-warrens often do swarm with fleas when the young rabbits are born, but this is presumably due to transfer of fleas from the adult rabbits, as part of the synchronization of the fleas with the hormones of the host, as has been clearly shown for the European rabbit-flea (M. Rothschild, 1965a, b). The splendid fleas of the Mexican volcano-rabbit, *Romerolagus* described by Barrera in 1967, defied discovery, despite intensive search of adult *Romerolagus* over a period of years, until the nestlings were located and examined.

G. The Association Between the Mode of Egg-Laying and the Nest-Flea Habit

Intimately associated with the pattern of behaviour exhibited by various kinds of fleas in locating a host, is the factor of the particular site where the flea-larvae transform into pupae and hence where the adults emerge. In this regard it is important to note that not all fleas deposit their eggs loosely amongst the hairs of the host as in the case of the cat- and dog-fleas (*Ctenocephalides*) (ix.1) so that the eggs may drop off anywhere in the haunts of the host. Some fleas, such as *Orchopeas howardi* (Baker, 1895) (iii.1) leave the host and glue the eggs to bits of debris in the nest and then return to the mammal. In the latter case, the immature stages are to be found in the nest, and that is where the newly emerged adults are to be found. This is why some species of fleas are common in the nests, especially at certain times of the year, even though they are not true nest-fleas in the sense we are using the term. I believe that *Stenoponia* and *Hystrichopsylla* are fleas that lay their eggs in the nest and hence are in this category, but real data are lacking. *Stenoponia* females are often noted with two huge eggs in the abdomen (as so beautifully depicted in a colour photograph by Sakaguti, 1962), in contrast to ceratophyllids, which may have 8–12 smaller, but fully developed ones. It would be surprising if *Stenoponia* could spew out such huge eggs while on the fur of an active host. Moreover, *Stenoponia* is a winter-flea, according to our observations in Pakistan and as indicated by available

and published records in the U.S.A. and Mexico, and adults are collected only during the cold season. The larvae apparently take nearly a year to develop, and the unmistakably large larvae can be seen in the rodent-nests in the summer, if not earlier. All these points suggest that the *Stenoponia* larvae could not find suitable conditions just anywhere, and that, instead, the life-cycle has become attuned for nest-development. In my view, this is also the case for other fleas which are frequently found in nests but which are modified along the lines of a fur-flea (and which Ioff (1929, 1941) has referred to as "nest fleas," along with the specialized fleas for which we used the term).

Vaschenok (1967), in fine detailed studies on the ecology and life-history of the pulicid *Echidnophaga oschanini* Wagner, 1930, has provided relevant observations along these lines, which also emphasize the physiological attunement of the flea to its host. This species lays its eggs only when in darkness, and since its host (*Ochotona*) is diurnal, the result is that the eggs are deposited only when the pika is in its burrow. Further, since the eggs are dry and non-adhesive, they immediately fall to the floor of the nest or lair, where there is an environment suitable for development of the larvae.

It is also clear that the egg-laying habits of the squirrel-infesting *Orchopeas*, mentioned above, are also adaptive, for adults emerging in the nest are ensured of food, especially during the breeding season, whereas larvae developing from eggs dropped indiscriminately from the fur of an active arboreal host may have a difficult time finding a suitable environment for development, as might the newly emerged adult flea in locating a squirrel. Thus it would seem that just as there are nest-fleas, so there may be nest-larvae, although so little is yet known about the larvae of most kinds of fleas that it is premature to discuss possible morphological or physiological differences between the free-living larvae and the nest-bound ones. The possible significance of the specific requirements for a nest environment for some species has been indicated in the first paper of this series (Traub, 1972a) when it was pointed out that the species of *Medwayella* infesting ground-squirrels had never (or extremely rarely) been collected on arboreal squirrels, and it is believed that the conditions in the nest account for these differences.

H. Reduction of Combs, etc. in Fleas other than Nest-Fleas

Inasmuch as the absence of combs and reduction in chaetotaxy is characteristic of many nest-fleas, it is desirable to refer to 3 families in which all members bear these features but are not nest-fleas in the ordinary sense, viz., the Vermipsyllidae (x), Coptopsyllidae (xiii) and Malacopsyllidae (xiv). The majority of species of Vermipsyllidae belong to the genus *Chaetopsylla* Kohaut, 1903, and all of which are parasites of carnivores, and are characterized by the following: large eyes; frequently fairly short mouthparts (but at times they are quite long, reaching the fore-trochanters); a well developed pleural arch and leathery, flexible abdominal segments, permitting great expansion. This unusual combination of characters can be explained by their habits—they are primarily den-fleas, specialized to feed for long periods on hibernating hosts during the winter months and early spring and/or when the young carnivores are born in the den. Presumably the eggs are laid loose among the fur of the

host (as in the case of the vermipsyllids mentioned below) and hence can fall off at any time and develop into larvae wherever the micro-environment is suitable, although many of these will be in the den. Many of the carnivores are diurnal, but the large eyes of the flea no doubt are also useful in enabling the newly hatched fleas to find their host, particularly if out-of-doors. As is to be expected, in the case of fleas infesting large mammals, especially if prone to hatch out on the ground, the vermipsyllids are good jumpers when unfed. Virtually all the records are from the cold parts of the year, or else are from alpine or subarctic heights in the mountains, indicating the species spend the rest of the year as eggs, larvae or pupae. The dense fur of the hosts enable these large fleas to hide easily if on the body, and to crawl with dispatch when grossly engorged.

The other two genera of vermipsyllids, *Vermipsylla* Schimkewitsch, 1885 and *Dorcadia* Ioff, 1946 are extreme in their adaptations for existence as "alakurts", grub-like fleas infesting the dense wool or thick patches of hair on the bodies of various ungulates in the high mountains of Central Asia. Very few fleas parasitize ungulates, probably because such hosts do not have dens or nests where the larvae have a good chance to develop, and the fleas an opportunity for a steady diet. Moreover, the hosts of the alakurt frequent forbidding terrain, and all in all, very few other kinds of fleas could possibly complete their life-cycles under such conditions. However, the alakurts emerge in the alpine fields and bogs at the onset of cold weather, when the horses, sheep, deer, etc. have dense coats, and the fleas, which have large eyes and are excellent jumpers, actively seek and leap upon their prey in daylight. (At night it is too cold for the fleas to move about, even if they were able to locate their hosts.) Their success, at least in the case of domesticated animals, is indicated by Ioff's report (1950) of 7000 specimens on a single sheep. In *D. dorcadia* (Rothschild, 1912), the size of the newly emerged female is stated to increase more than 250-fold as it engorges on its host and as the eggs mature (Ioff, 1950). The males remain active on the host and do not feed much, but the females remain *in situ* on the host for very long periods (as expected in fleas with such long mouthparts). Grossly-swollen females can crawl maggot-like, or by a wiggle induced by peristalsis-like waves, since they are too fat to use their legs. *Dorcadia* have been observed to remain on a single host for 3 months although moving about from time to time. The eggs are deposited loosely amongst the hairs or wool, and eventually fall to the ground, where the eggs may remain viable but unchanged all winter. The larvae emerge in the spring, feed on organic debris, often in clumps of dried sod, and pupate in the late summer or fall. It is of interest that these larvae, which may hatch out in the open, are believed to have a rudiment of an eye (Ioff, 1950) unlike other known flea-larvae, which are generally in the dark.

It is important to note that the Vermipsyllidae are believed to have always been without combs of spines (at least on the pronotum), unlike the families of fleas we have been discussing heretofore (Jordan, 1947; Holland, 1949; Traub & Evans, 1967),[10] and thus only superficially resemble the nest-fleas which have lost the combs by reduction. As can be seen from the above outline, the vermipsyllids differ likewise in other details of structure, habits and hosts—one notable development is the labial palpus of 25 joints in *Dorcadia*, instead of the 5 segments seen in most fleas.

The Coptopsyllidae are another family that may have lacked combed ancestors since none of the species possess even apical spinelets on the abdomen, and there is no trace of genal or pronotal combs. One species even lacks the mesonotal pseudosetae which is supposed to represent a rudimentary (incipient) ctenidium—a condition that is rare in most families of the Order. Here again the low number of abdominal bristles and the presence of very long mouthparts are suggestive of nest-fleas, but the large eye and frequent presence of extremely long tibial bristles, and the supernumerary plantar tarsal bristles are not. Moreover, the abdominal bristles are often long. The marked length of the tibial bristles is suggestive of other desert-fleas, e.g. some *Xenopsylla*, where Ioff (1941) believed they were used in burrowing into the sand to enable the flea to escape the sun and heat. The pleural arch is large and hence although the lateral metanotal area is higher than long, I believe they may be fair jumpers. As Lewis (1964) points out, a fairly large number of species have been described, but only a few specimens have ever been collected, in most instances. Too little seems to be known about their habits to warrent further discussion.

The Malacopsyllidae (xiv) include 2 South American monotypic genera, *Malacopsylla* and *Phthiropsylla*. These, although combless or essentially so, and with reduced vestiture are obviously modified as "sticktight" fleas, i.e. to stay attached to the host for long periods and feed until swollen with blood (hence the specific name *M. grossiventris* proposed by Weyenbergh, 1879). Thus, the cuticle is leathery and bears longitudinal pleats, permitting great expansion, while the tibial bristles are extremely short and stout, as are some of the tarsal bristles, and even the plantar bristles are stout or even subspiniform. The eye is large and the pleural arch well developed, indicating these fleas seek out their prey, leap upon them and catch and hold on by means of the specialized tibiae and tarsi, and therefore are not nest-fleas. These conclusions are the same as those reached by Johnson (1957). The sticktight habit recalls the case in the Pulicidae (ix), where the hectopsyllines and many of the Pulicinae are combless, have large eyes, are excellent jumpers and are fixed or semisessile on the host (but which stay attached by means of anchoring mouthparts).

I. The Possible Relation Between the Pronotal Comb and a Frigid Environment

Smit & Dunnet (1962) in remarking on the facts that in the Antarctic *Glaciopsyllus antarcticus*°, the pronotal comb is represented only by pseudosetae (or by apical spinelets), and in the Arctic *Mioctenopsylla* is greatly reduced (i.e. the spines are extremely small and pale), stated that "there may conceivably be a partial correla-

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[10] It is not clear as to whether Jordan (1947) meant that the vermipsyllids never had any combs on any of the segments or if he had only the pronotum in mind. Combed fleas always seem to have at least the pronotal comb, and Jordan believed that the pseudosetae represent incipient combs. It would therefore seem that the presence of pseudosetae on the pronotum, which is the case in vermipsyllids, rules out the possibility that the ancestor of that flea had a pronotal comb, and it would then follow that the ancestral flea lacked other combs as well. This may very well be the case, but the Antactic flea *Glaciopsyllus antarcticus*° is unique in the family Ceratophyllidae. in lacking a pronotal comb, and presumably has pronotal pseudosetae, yet apparently all students of Siphonaptera believe it is descended from combed fleas. However, the prothorax seem to bear seta-like apical spinelets as well (Traub & Evans, 1967), and the relationship between these and true pseudosetae, or the structure resembling pseudosetae in this species, requires further study. If there are no true psuedosetae on the pronotum and the spinelets represent vestigial spines, Jordon may be correct.

tion between temperature and development of ctenidia". This is an interesting possibility and more information is needed before it can be evaluated. However, data at hand lead me to question it. None of the fleas collected by us in Arctic terrain at 12000 ft elevation in the Himalayas of West Pakistan, where the ground is frozen 9 months of the year and where it may snow in summers (Traub & Evans, 1967), showed any such tendency. Thus, in species like *Ctenophthalmus golovi* Ioff & Tiflov, 1930 (i.3) and *Frontopsylla elata* (Jordan & Rothschild, 1915) (iv.2), the combs are similar to allied forms, instead of being reduced, although it is true that these species are also found in less frigid climes and hence may not be valid examples. However, *Monopsyllus thambus* (Jordan, 1929) (iii.1) is a flea of the far north and of subartic heights in the Rocky Mountains, and it can be seen by comparing fig. 57 with that of fig. 59 (*M. wagneri*, another *Peromyscus*-flea, but a temperate one), that there is no reduction in the comb. Alaskan and other northern fleas show no loss regarding number or size of spines unless they are nest-fleas.

Perhaps there is more reason to believe that the reduction of the comb seen in *Mioctenopsylla* and *Glaciopsyllus*° Smit & Dunnet, 1962 is correlated with the fact that other fleas of sea-birds lack combs, viz. *Notiopsylla* (ii.1), *Actenopsylla* (ix.1), *Ornithopsylla* (ix.1), 3 species of *Xenopsylla* (ix.1) and *Parapsyllus* Enderlein, 1903 (iv.2).[11] Further, *Notiopsylla* is highly exceptional amongst pygiopsyllids in not bearing ctenidia, while *Actenopsylla* and *Ornithopsylla*, spillopsyllines, are the only members of their subfamily with this trait. However, no *Xenopsylla* bear combs and no rhopalopsyllid (to which family *Parapsyllus* belongs) has a true ctenidium either. As indicated above, I believe the reduction of the comb seen in these bird-fleas is associated with their being primarily nest-fleas.

J. Structural and Behavioural Variety Within a Uniform Order of Insects

The Order Siphonaptera is so distinctive and basically uniform that Snodgrass (1946) pointed out that even any small piece of the exoskeleton of a flea can be promptly recognized without question. Yet, within this overall plan, believed to be of undoubted monophyletic origin (Jordan, 1947), much more diversity exists in behaviour and structure than is generally appreciated. There are the hypodermal Tunginae like *Tunga*, which are so specialized that the tiny females penetrate into the superficial layers of the skin of the host and ultimately lie almost completely within a cyst, with just the apex of the abdomen protruding. Here the flea may remain for weeks, engorging on blood repeatedly, and as the abdomen fills with dozens of eggs, the females may reach the size of a pea, extruding eggs to the outside world intermittently. The sticktight fleas (other Tunginae and the pulicine *Echidnophaga*) act in a somewhat similar way but remain external, anchored by long serrate mouthparts. In both groups combs of spines are absent, and the vestiture

[11]*Parapsyllus* is a member of the Rhopalopsyllidae, all of which lack true combs, and hence the absence of a comb in this genus may have nothing to do with the parasitism of sea-birds. On the whole, the family infests rodents and is essentially Neotropical, but one other genus may also be associated with sea-birds, namely the Argentinian *Listronius* Jordan, 1942, which includes 3 species all of which are known only from 1 or 2 specimens. One of these species, *L. robertsianus* (Jordan, 1939), has been found only in the Falkland Islands, on two occasions, once in the burrow of sea-birds and once on an ornithologist.

reduced in general; the thorax is extremely narrow and telescoped; the head very large and angulate, so that it may be pressed against the host as the flea attaches; while the abdomen is capable of marked extension.

Others like the pulicine rabbit-fleas are sessile only for certain periods and move about occasionally to a new site or to move onto the young of the host. The vermipsyllids and malacopsyllids, like the tungines, have a leathery integument and hence are capable of gross enlargement, but they are external ectoparasites and not as fixed. Other attributes of these fleas have already been mentioned. Many kinds of fleas are active on the host, and move about and feed frequently, like the familiar cat-fleas. These are fur-fleas, and possess combs of spines and rows of stiff backward projecting bristles to enable them to remain safely on the host. Variants on this theme, occurring throughout the Order, possess spiniforms or other modified types of bristles along or near the front margin of the head so that they can hook onto hairs while feeding or resting (Traub, 1968). Such "thorny-headed" fleas are further adapted in having the head flattened and in possessing stout procoxae, modifications which enable them to appress their heads against the body of the host while hooked onto the bases of hairs (Traub, 1968, 1969). Most of the above types of fleas have a well developed pleural arch and are good jumpers, enabling them to, at least, find a host before becoming fixed, or in the case of some of the fur-fleas, to locate a second one after leaving the first to lay eggs, etc. In the case of hypodermal or sticktight fleas with ready access to hosts, to which they remain affixed for life, the pleural arch is greatly reduced. Those of diurnal hosts have large eyes. In contrast, are the nest-fleas, marked by reduction of eyes, combs, chaetotaxy, and thorax, as we have seen, and which presumably glue their eggs to debris in the nest rather than deposit them loosely among the hairs of the host. It should be borne in mind that fleas which are closely related taxonomically may vary considerably with respect to habit (and, accordingly, in habitus, to some degree). This is at times true of species placed in the same genus, e.g. *Chimaeropsylla* Rothschild, 1911 (xi.1) and also *Ceratophyllus* (iii.1). As N. C. Rothschild (1911) and Smit (1952) pointed out, *Chimaeropsylla potis* Rothschild, 1911 is modified as a sticktight flea, as indicated by the presence of broad, coarsely serrate laciniae and modifications in the head, in which the fronto-clypeal region is shortened and the genal region lengthened. With a head of this type, the anchoring mouthparts may be swung in position as to be almost horizontal when embedded in the host, and be remote from the maxillary palpi. In contrast, in *Chim. haddowi* Smit, 1952, as that author has shown, the head is rounded, the genal-frontoclypeal regions are of comparable size and the stylets are narrow, suggesting this species is not truly a sticktight flea. The amplitude of swing of the mouthparts of *C. haddowi* is too great for a normal free-living flea, however, and hence Smit believes that species is tending towards "a sedentary life".

M. Rothschild & Hinton (1968) provide interesting support for Smit's belief that *C. potis* is a sticktight flea but *C. haddowi* is not, and this evidence is based upon their demonstration of a significant correlation between special adhesive discs on the antenna of male fleas and the degree of fixation of the female. During copulation, males of most species grasp the abdomen of the female by means of their elevated, long antennae, and Rothschild & Hinton believe that the discs help restrain the

female during the act. These adhesive holding-structures have been noted in all but one of the recognized families of fleas (but not necessarily in all representatives thereof), and they are apparently well developed in species in which the females are active and mobile at the time of pairing. In the sessile fleas whose mating-habits have been observed, either the male antennae cannot be employed to grasp the female because of their structure and position, or else they lack the adhesive discs. Thus, in the European rabbit-flea, *Spilopsyllus cuniculi* (ix.1) the males grasp the females by their antennae while mating, but they lack the adhesive discs, as do the related species of the New World rabbit-fleas of the genus *Cediopsylla* Jordan, 1925. It is noteworthy that these female rabbit-fleas are essentially sessile at the time of mating. What is particularly relevant to the case of *Chimaeropsylla* is that the adhesive discs are lacking in *C. potis* but present in *C. haddowi*, as Rothchild & Hinton point out.

As M. Rothschild has stated (*in litt.*) the convergence between *Spilopsyllus* (and *Cediopsylla* as well) and *C. potis* is quite striking. In all three taxa, the frons is angled, the laciniae are stout and markedly serrate and the cuticula is dorsally incrassate and at times leathery elsewhere. All of these features are often seen in sticktight fleas. The 3 genera also agree in that both genal and prothoracic ctenidia are present, the eye is relatively large and the pleural arch is well developed. The last two features are characteristic of fleas of active diurnal hosts, and the chunky, stout body seen in these genera also suggests species that must seek such a host, just as the ctenidia recall the need to remain thereon once it is found, before the fleas become semi-sessile.

Fleas of the genus *Ceratophyllus* are particularly instructive in that marked behavioural and structural differences may occur even amongst species parasitizing the same kind of host, and hence the swallow-fleas of this genus are discussed in some detail.

Darskaya (1954b, 1959, 1964a) in a series of interesting articles on the subject, has classified the Palaearctic ceratophyllid bird-fleas into two ecological groups on the basis of the correlation of the behaviour of the fleas with the habits of the particular birds they parasitize. On the one hand are the "settled" fleas, which have a relatively pronounced host-specificity and can survive long periods of starvation in the nest after the birds have reared their young in the spring and have all departed. These are epitomized by the swallow-nest fleas which are poor jumpers and do not emigrate. Since the hosts of these fleas seldom alight, and even feed while flying, the inability of these fleas to leap well, and their disinterest in leaving the nest burrows, are adaptive advantages. If fleas of this class ever did fall to the ground, away from the nest-site, they would have virtually no chance of finding their specific hosts nor of returning to the nest. In the spring, however, some of these fleas may be carried by the birds from one nest or colony to another, before the birds settle down for nesting, but this particular kind of flea does not remain on the host for long periods.

During the spring and summer, the "settled" fleas generally produce only one generation. Possession of a very large fat-body, with stored nutriment, enables them to survive the long period (as much as 10 months) while they are nest-bound in the absence of the birds. During the winter, their body-functions are slowed as the

fleas remain inactive in cracks in the nest. With the onset of warm weather in the spring, and the annual return of the birds, the fleas become very active, suck blood from the host avidly and quickly and rapidly mate and produce eggs. The larval stage is accelerated so the life-cycle is completed while the birds are still in the nest, giving the new crop of adults time to engorge on blood before the long siege begins. Inasmuch as the young birds likewise develop rapidly, and these birds have only one brood a year, an abbreviated span for the reproductive and developmental stages is a necessity.

Morphologically, the "settled" fleas are light in pigmentation or exhibit the characteristic banded appearance reported by Holland (1952) for *C. arcuegens*°. This is due to the anterior portions of the abdominal segments (both terga and sterna) being well sclerotized, or even especially so, while the posterior regions are lightly tanned. The former attribute offers protection to the body when the flea crawls into tight crevices in the nest; the latter permits gross enlargement of the abdomen as the fat-body enlarges. The alternating brown and light bands on the abdomen often enables one to recognize the specimens as bird-fleas even with the naked eye. This group of fleas is also characterized by relatively small (but nevertheless well developed) eyes, reduction or loss of sclerotization of the metanotal flange or "collar" (permitting flexibility of the abdomen in crawling, and scope in enlarging) and reduction or loss of the pleural arch, with concomitant lessened ability to jump and increased facility to crawl into crevices. Many of these attributes have been shown above to be characteristic in general of nest-fleas, and as indicated by Holland (1952) and Darskaya (1964a, b). Examples of fleas of this type are *C. delichoni*°, which lacks the pleural arch and *C. hirundinis*, in which it is present.

In contrast to the "settled" fleas are the bird-fleas which Darskaya calls "nomadic" or "migrating" (1954a, 1959, 1964a). (Perhaps in English, "perambulatory" may be a better term, avoiding the connotation of a fixed direction or a return, and yet indicate a purpose for the movement.) In this category are *C. garci* Rothschild, 1902 and *C. gallinae* (Schrank, 1803) which usually parasitize birds which do not return to utilize nests of the previous year, and hence any fleas which had hatched out in such a nest are faced with the problem of finding a bird to infest. This is solved by leaving the nest and actively seeking a host. *C. styx* (whose host, the sand-martin, generally does return to its old nest-site in the spring) leave the burrows in which they were born and may travel as much as 50 feet to another and new nest-site, "recognize" it, and settle there (Bates, 1962; M. Rothschild, 1969). This species, which is an excellent jumper and can span 200 mm (M. Rothschild, 1969), has the facility of immediately leaping onto a bird which hovers for a few seconds near the nest, and it seems likely that other bird-fleas can act similarly.

Perambulatory fleas usually have the ability to feed on a variety of hosts, enabling them to effectively parasitize nearly any bird they find. It is not surprising that fleas which have to be highly mobile to survive are: 1. excellent jumpers and climbers and fast walkers; 2. have large eyes; 3. well developed thoraces, including a large pleural arch; and 4. are almost black in colour due to the heavy tanning of the cuticle. The "nomadic" fleas overwinter in the cocoons and must feed soon

after emergence or starve. The fat-body is small and is rapidly consumed during the summer, and the fleas feed frequently and quickly. Several generations are produced a year, since the hosts also tend to raise more than one litter annually. The flea-population in such nests can build up to enormous proportions.

Darskaya's notable observations were necessarily based upon study of a limited number of species of *Ceratophyllus* in the U.S.S.R. and dealt with a variety of complex and little-known phenomena. Even so, her generalizations, in the main, apply well to bird-fleas from other parts of the world and to other taxa, as will be shown shortly. As is to be expected, however, some species that have certain of the attributes of "nomadic" fleas exhibit a pattern of behaviour somewhat different from that of *C. garei*, etc. For example, they conform with respect to the morphological features noted above and in that these fleas appear to spend little or no time in the nests as adults, and actively seek their hosts. These fleas, however, apparently spend most of their adult lives on the birds themselves and hence, as pointed out by M. Rothschild (*in litt.*) are analagous to the "body-fleas" or "fur-fleas" of mammals. Such fleas presumably can accompany a bird on migrations of thousands of miles. Thus, the Holarctic *Dasypsyllus gallinulae* (Dale, 1878) (iii.1) has not only been found in North America and Europe but in such extremes as Panama and the Far North, and in regions as distant as the Philippines (Traub, 1950b), North Borneo and Malaya. I was surprised to collect the "arctic" species *Dasypsyllus stejnegeri* (Jordan, 1929) in central Mexico, but Smit (1961) reported it from the Falkland Islands! The Panama records of *D. gallinulae* were based upon specimens Dr. H. C. Matthes collected from a sudden infestation on his own body, while walking in the forest of Mt. Volcán. It therefore seems likely that this is a perambulatory species.

In all probability, other bird-fleas, whose habits have not yet received the type of intensive study undertaken by Darskaya for Palaearctic *Ceratophyllus*, could be divided into similar ecologic groups. The Antarctic flea, *Glaciopsyllus*° and the spilopsylline fleas of sea-birds are in the category of "settled" fleas, as indicated above. *Lentistivalius insolli* (ii.1) with its brown and white banded appearance, relatively small eye and records of collections from nests rather than birds, presumably is in this category. Fleas of the genus *Hoogstraalia*, which possess a genal ctenidium, and are darker in colour, etc., may be "perambulatory" fleas.

Although the ecology of rodent-fleas has not been studied as well as that of bird-fleas, because of the inherent difficulties, a great deal of fine work has been done in the Soviet Union on this subject. It is apparent that the behaviour of the rodent-fleas is as specialized and complex, and as inter-related with the habits of the host as the bird-fleas mentioned above. For example, several species of fleas with well developed eyes have been noted to swarm to and about the burrow-opening, pursue prospective hosts or "emigrate" into new burrows if their birth-places had been abandoned by the rodents (Darskaya, 1954a, 1955, 1964b; Ioff, 1941).

K. The Principle of Structural Compensation

It has been pointed out that in Siphonaptera the total mass of two or more structures that are associated in a common function generally is a theoretical con-

stant (Traub, 1969). For example, the claspers, which operate as a unit in grasping the female in copulation, may be of approximately equal size, or else the movable finger (F.) may be enlarged while the immovable process (P.) is small, or thirdly, F. may be reduced and P. huge. It was also shown that the relative size of Ford's sclerite varies inversely with the comparative degree of development of the crochets or of ventral paramere-like processes. In other words, although the size of the individual components may vary, they do so inversely, in a correlated manner, and, in effect, the total amount of tissue-substance involved is the same, and the over-all functional result is apparently not impaired. The specimens collected by Lord Medway's team on Gunong Benom, and the other material discussed in the previous article in this series (Traub, 1972a), also provide interesting examples of this principle.

Particularly relevant are the unusual specializations cited and illustrated for each sex of *Stivalius cognatus* Jordan & Rothschild, 1922 (a member of *Stivalius* Jordan & Rothschild, 1922 *s. str.*). It will be recalled that in the previous article it was emphasized how the sclerotized inner tube (S.I.T.) is characteristically elongated in that taxon and that Ford's sclerite (F.SC.) is greatly enlarged, while, in contrast, the paramere-like ventral process of the crochet is vestigial or totally absent. The situation is very different in most members of *Stivalius s. lat.*, which have well developed ventral crochet-processes (CR.P.), and in which S.I.T. is short and broad in comparison, i.e. *Medwayella* and *Lentistivalius*, as figured in that article. It was therefore suggested that the hypertrophied Ford's sclerite and highly elongate S.I.T. serve to replace, in function, the ventral "parameres," which have been lost in the course of evolution. That the reduction of CR.P. and concomitant modifications of S.I.T. and of F.SC. are in accord with this principle of structural compensation is further suggested by developments in other members of *Stivalius s. lat.*, viz. *S. jacobsoni* Jordan & Rothschild, 1922 and *Parastivalius novaeguineae* (Rothschild, 1904). These two are in the minority of "*Stivalius*" in which the aedeagus lacks ventral caudad-directed, finger-like or rectangular processes, and in each case there is a unique alternate device that appears as an apparent substitute. Thus, *S. jacobsoni* is one of the few species in which the very apex of the dorsal wall of the end-chamber of the aedeagus is highly modified, in this case being produced into 2 highly acuminate fang-like projections. In *P. novaeguineae*, the ventral armature of S.I.T. is not only displaced far caudad, but it is hook-like suggesting a crochet in appearance.

If the principle of structural compensation is a sound one, then it would be expected that there would be intermediate species in which the cooperating members of the functional device were only partially modified, e.g. there would be varying degrees of development of alternate mechanisms. *S. phoberus* (Rothschild, 1904) is an example of such an intermediate form, since, as has been shown in the previous article in this series, S.I.T. is not nearly as elongate as in other members of the genus (*Stivalius s. str.*), and the vestige of the crochet-process (CR.P.) is longer than in its allies. What then compensates for the loss of the functional part of CR.P., the ventral caudad-directed "parameres"? It is noteworthy in this regard that several of the associated sclerites seem more highly developed in *S. phoberus* than in related fleas with the ophidian-like S.I.T. Thus: (1) F.SC. bears 2 apical hooks per side, not 1. (2) S.I.T. has a longer and broader apical fistula (FIS.) which is tanned to a

greater degree than in *S. cognatus*, etc. FIS. in *S. phoberus* also appears to have more discreet tanned borders *within* S.I.T. (and may prove to be protrusible, at least here, if not throughout the genus).

Another relevant example of the principle of compensation is provided by the metasternal furca, as has been indicated by M. Rothschild (*in litt.*). In fleas which have lost the pleural arch, the furca is hypertrophied, as in the case of *Wenzella*° (fig. 85, I.F.–3) and *Conorhinopsylla*° (fig. 86). This tendency is even exhibited in members of the same genus which differ with respect to the development of the pleural arch and ridge, e.g. *Opisodasys* and *Ceratophyllus*, and is presumably associated with the attachment of muscles which ordinarily fasten to the pleural ridge when the arch is present.

The principle of compensation actually seems to apply to more than adjacent or cooperating structures or organs, for the extreme modifications of the hypodermal and sessile fleas (Tunginae) presumably fit the concept. Here the head and mouthparts have become enlarged or greatly strengthened, and the abdomen capable of enlarging enormously, while the thorax has become so tremendously compressed that it is difficult to discern its components.

The Principle of Structural Compensation is a corollary of the Principle of Totality of Mass (Traub, 1969), which states that while the components of a structure may vary in size or mass, the over-all size is a relative "constant". Thus, in some species the pronotal spines are long, while the pronotum is narrow, as in figs 18 and 21; in others, the reverse is true (fig. 63). The latter principle is well illustrated by a species treated above as an example of a flea undergoing reduction of ctenidia, namely *Trichopsylloides oregonensis*°. Here the genal ctenidium is usually entirely absent, or else is represented by but 1 or 2 tiny pale spines. It is noteworthy that the gena itself is unusually large and overlaps the base of the procoxa. It thus encompasses the same area as does the fully developed comb of the related genus *Rhadinopsylla*°.

V. CONCLUSIONS

Fleas are far more specialized for their particular mode of life than had been realized a few years ago, not only with respect to their behaviour and physiological responses, but also concerning their morphology. All of these phenomena are intimately related to corresponding features of their host and bespeak of an ancient and intimate association between parasite and host, even to the point of evolving together, as witness the fit of the pronotal combs of some fleas to the hairs of the mammal they infest. In other instances, the pronotal comb and structure of the thorax and degree of development of the eye, reflect the environment and habits of the host and the corresponding modifications of the flea thereto.

The adaptive responses of the Siphonapteran pronotal comb to the pattern of the hairs of the host, and the association between the structure of the metathorax and the advantages or disadvantages of the ability to leap, are examples of the moulding-influence of the environment, which tends to result in uniformity of physiognomy, despite the fact that different mechanisms may have been employed to achieve these ends. Such modifications in fleas therefore parallel the remarkable conver-

gences seen almost everywhere in nature, viz., the amazing similarity in appearance of carnivorous marsupials and the placentate Carnivora even though the two represent two independent lines of evolution.

It is apparent that there still is a great deal to be learned about some of the principles involved in the examples of convergent evolution and adaptations mentioned, to say nothing of the details. Some of the many unanswered questions could be resolved if more were known about the flea-fauna of South America, Australia and the Australo–Indonesian Archipelago, and about host-relationships in general. Even more, we require data on the ecology of fleas and mammals and birds, and study of living material.

VI. ACKNOWLEDGEMENTS

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VII. LIST OF TAXA CITED IN TEXT

Code	*Family*	*Code*	*Subfamily*
i.	Hystrichopsyllidae	1	Hystrichopsyllinae
		2	Anomiopsyllinae
		3	Ctenophthalminae
		4	Dinopsyllinae
		5	Doratopsyllinae
		6	Listropsyllinae
		7	Neopsyllinae
		8	Rhadinopsyllinae
		9	Stenoponiinae
ii.	Pygiopsyllidae	1	Pygiopsyllinae
		2	Lycopsyllinae
iii.	Ceratophyllidae	1	Ceratophyllinae
		2	Foxellinae

iv.	Leptopsyllidae	1	Leptopsyllinae
		2	Amphipsyllinae
v.	Ischnopsyllidae	1	Ischnopsyllinae
		2	Thaumapsyllinae
vi.	Rhopalopsyllidae	1	Rhopalopsyllinae
		2	Parapsyllinae
ix.	Pulicidae	1	Pulicinae
		2	Tunginae
x.	Vermipsyllidae		—
xi.	Chimaeropsyllidae	1	Chimaeropsyllinae
		2	Chiastopsyllinae
xiii.	Coptopsyllidae		—
xiv.	Malacopsyllidae		—
xv.	Xiphiopsyllidae		—

° The °, if applicable, precedes the name in this List for convenience in scanning, whereas in the text it follows the name.

VIII. LIST OF HOSTS

Allactaga Cuvier, 1836
Aplodontia Richardson, 1829
Apodemus Kaup, 1829
Arctictis binturong (Raffles, 1821)
Arvicanthis Lesson, 1842
Bathyergus Illiger, 1811
Callosciurus Gray, 1867
,, *erythraeus* (Pallas, 1778)
Calomyscus Thomas, 1905
Citellus Oken, 1816
,, *dauricus* Brandt, 1843
Cryptomys Gray, 1864
Cynomys Rafinesque, 1817
Dremomys Heude, 1898
Erinaceus Linnaeus, 1758
Eutamias Trouessart, 1769
Felis bengalensis Kerr, 1792
Heteromys Desmarest, 1817
Hylopetes Thomas, 1908
Hyperacrius Miller, 1896
Lariscus Thomas & Wroughton, 1867
Marmota Blumenbach, 1779
Martes Pinel, 1792
Meriones Illiger, 1811
Microtus Schrank, 1798
Mus Linnaeus, 1758
Myospalax Laxmann, 1769
Neotoma Say & Ord, 1825
Neotomodon Merriam, 1898
Ochotona Link, 1795
Octomys Thomas, 1920
Onychomys Baird, 1857
Oryzomys Baird, 1857
Otomys unisulcatus Cuvier & Geoffroy, 1829
Peromyscus Gloger, 1841
Petaurus Shaw & Nodder, 1791
Petrochelidon Cabanis, 1850
Pogonomys Milne-Edwards, 1877
Ptychorhamphus M. Brandt, 1837
Puffinus Brisson, 1760
Rattus Fischer, 1803
Rattus (*Rattus*) Fischer, 1803
Reithrodontomys mexicanus Saussure, 1860
Rhinosciurus Gray, 1843
Rhombomys Wagner, 1841
Romerolagus Merriam, 1896
Sciurus Linnaeus, 1758
,, *granatensis chiriquensis* Bangs, 1902
Spalax Guldenstaedt, 1770
Tachyglossus Illiger, 1811
Tamias, Illiger, 1811
Tamiasciurus Trouessart, 1880
Tupaia Raffles, 1821

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X. INDEX[13]

[13] Numerals preceded by 'T' refer to Table 1. Numerals preceded by 'F' refer to figures. Allusions to hosts frequently pertain to the fleas of those animals. (For references to scientific names of fleas, see the LIST OF TAXA CITED IN TEXT.)

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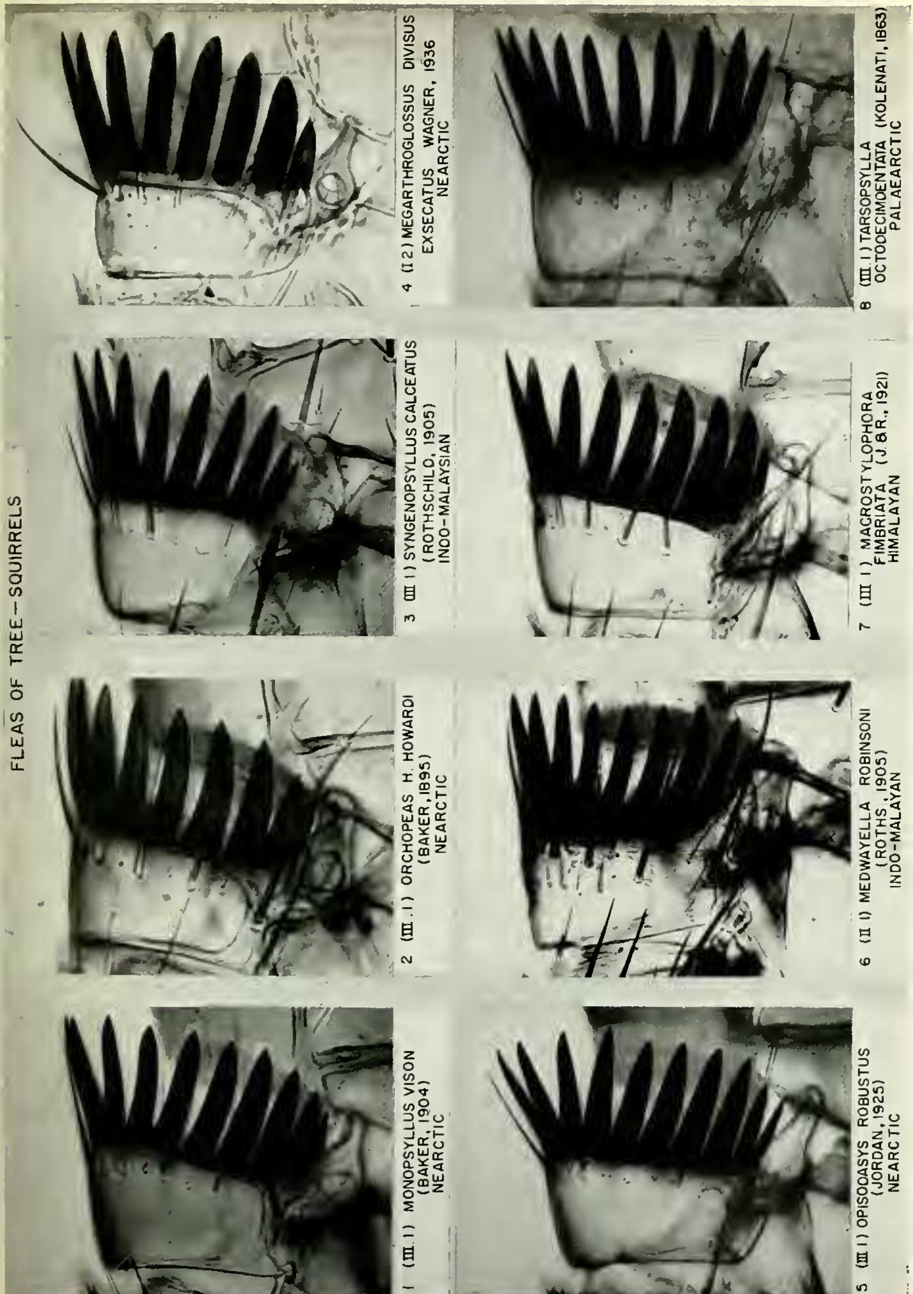
PLATE I

Fleas of Tree-Squirrels

Fig. 1. (iii.1) *Monopsyllus vison* (Baker, 1904) Nearctic
Fig. 2. (iii.1) *Orchopeas h. howardi* (Baker, 1895) Nearctic
Fig. 3. (iii.1) *Syngenopsyllus calceatus* (Rothschild, 1905) Indo-Malaysian
Fig. 4. (i.2) *Megarthroglossus divisus exsecatus* Wagner, 1936 Nearctic
Fig. 5. (iii.1) *Opisodasys robustus* (Jordan, 1925) Nearctic
Fig. 6. (ii.1) *Medwayella robinsoni* (Rothschild, 1905) Indo-Malayan
Fig. 7. (iii.1) *Macrostylophora fimbriata* (J. & R., 1921) Himalayan
Fig. 8. (iii.1) *Tarsopsylla octodecimdentata* (Kolenati, 1863) Palaearctic



FLEAS OF TREE-SQUIRRELS

1 (III.1) MONOPSYLLUS VISON (BAKER, 1904) NEARCTIC

2 (III.1) ORCHOPEAS H. HOWARDI (BAKER, 1895) NEARCTIC

3 (III 1) SYNGENOPSYLLUS CALCEATUS (ROTHSCHILD, 1905) INDO-MALAYSIAN

4 (I 2) MEGARTHROGLOSSUS DIVISUS EXSECATUS WAGNER, 1936 NEARCTIC

5 (III 1) OPISODASYS ROBUSTUS (JORDAN, 1925) NEARCTIC

6 (II 1) MEDWAYELLA ROBINSONI (ROTHS., 1905) INDO-MALAYAN

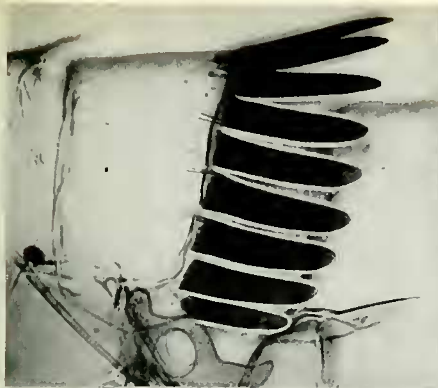
7 (III 1) MACROSTYLOPHORA FIMBRIATA (J.&R., 1921) HIMALAYAN

8 (III.1) TARSOPSYLLA OCTODECIMDENTATA (KOLENATI, 1863) PALAEARCTIC

PLATE 2

Fleas of Tree-Squirrels

FIG. 9. (iii.1) *Aenigmopsylla grodekovi* Sychevsky, 1950 Palaearctic
FIG. 10. (iii.1) *Kohlsia graphis* (Rothschild, 1909) Central America
FIG. 11. (iii.1) *Nosopsyllus ceylonensis* Smit, 1953 Ceylon
FIG. 12. (iii.1) *Pleochaetis soberoni* Barrera, 1958 Mexico
FIG. 13. (iii.1) *Libyastus infestus* (Rothschild, 1908) Ethiopian
FIG. 14. (iii.1) *Macrostylophora hastata* (J. & R., 1921) Indo-Malayan



9(III.1) AENIGMOPSYLLA GROOEKOVI SYCHEVSKY, 1950
PALAEARCTIC

10(III.1) KOHLSIA GRAPHIS (ROTHSCHILD, 1909)
CENTRAL AMERICA

11(III.1) NOSOPSYLLUS CEYLONENSIS SMIT, 1953
CEYLON

12(III.1) PLEOCHAETIS SOBERONI BARRERA, 1958
MEXICO

13(III.1) LIBYASTUS INFESTUS (ROTHSCHILD, 1908)
ETHIOPIAN

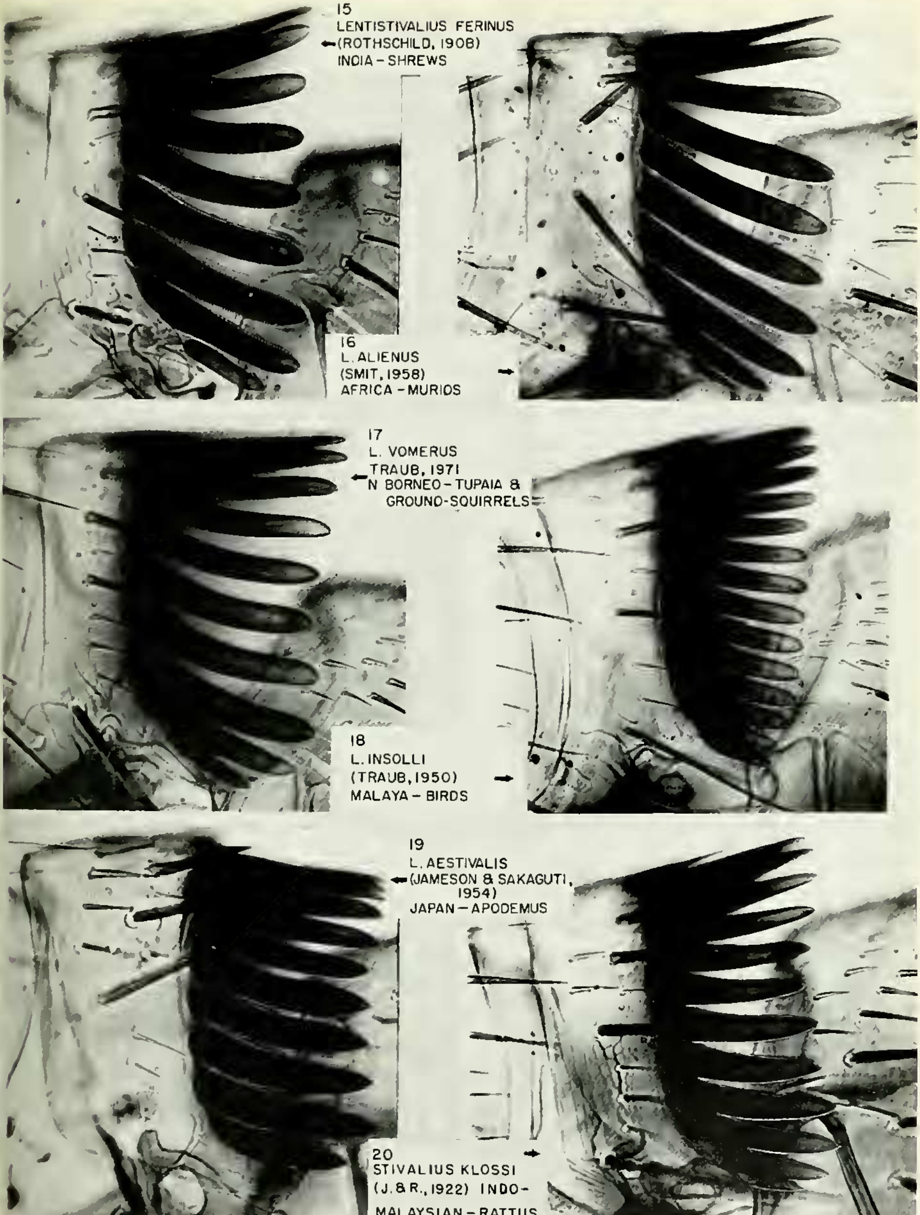
14(III.1) MACROSTYLOPHORA HASTATA (J. & R., 1921)
INDO-MALAYAN

FLEAS OF TREE-SQUIRRELS

PLATE 3

Variations in Pronotal Combs **Lentistivalius** and an Allied Taxon (ii.1)

FIG. 15.	*Lentistivalius ferinus* (Rothschild, 1908) India—Shrews
FIG. 16.	*L. alienus* (Smit, 1958) Africa—Murids
FIG. 17.	*L. vomerus* Traub, 1972 N. Borneo—*Tupaia* and Ground-Squirrels
FIG. 18.	*L. insolli* (Traub, 1950) Malaya—Birds
FIG. 19.	*L. aestivalis* (Jameson & Sakaguti, 1954) Japan—*Apodemus*
FIG. 20.	*Stivalius klossi* (Jordan & Rothschild, 1922) Indo-Malaysian—*Rattus*



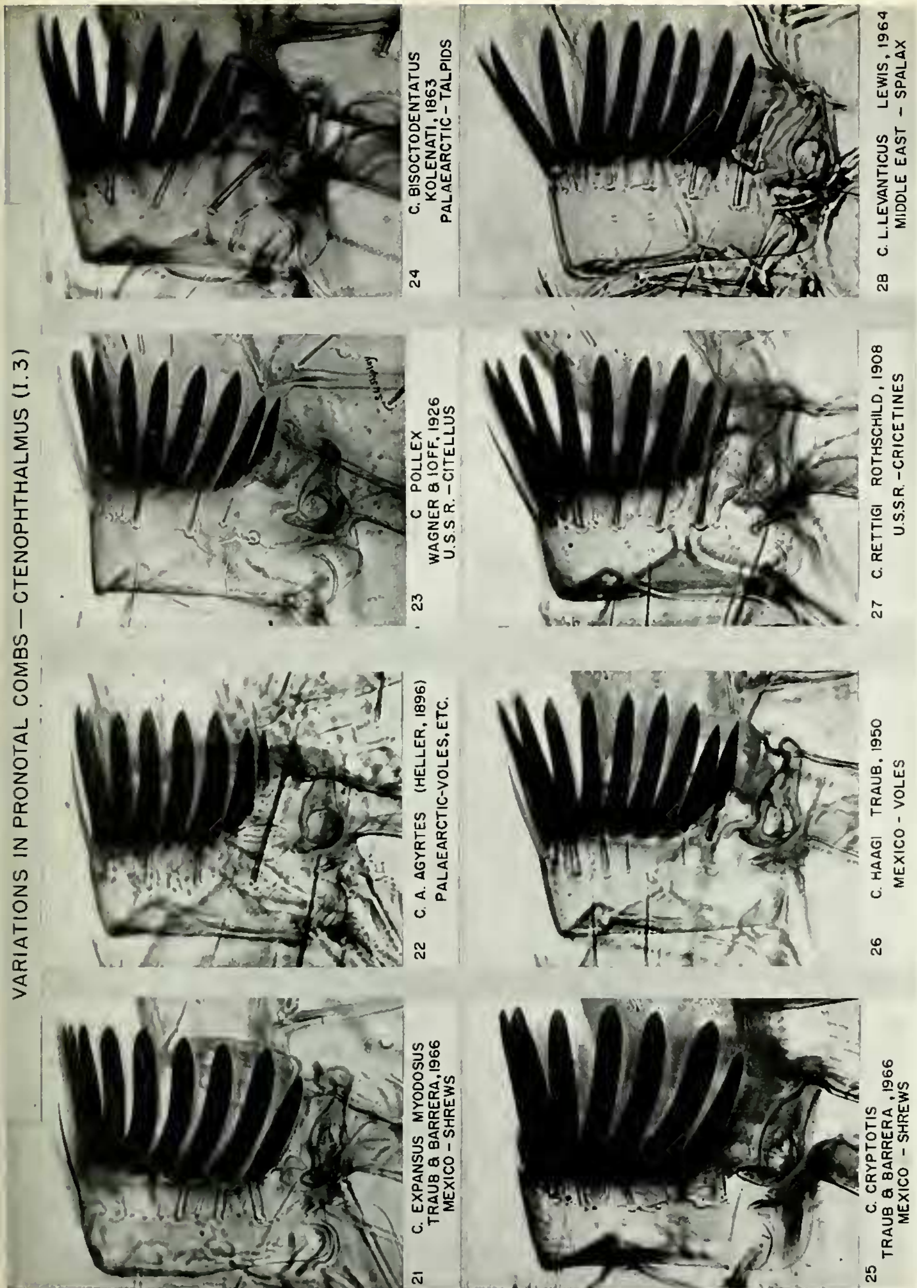
VARIATIONS OF PRONOTAL COMBS - LENTISTIVALIUS AND AN ALLIED TAXON (II.1)

PLATE 4

Variations in Pronotal Combs—**Ctenophthalmus** (i.3)

FIG. 21	*C. expansus myodosus* Traub & Barrera, 1966 Mexico—Shrews
FIG. 22.	*C. a. agyrtes* (Heller, 1896) Palaearctic—Voles, etc.
FIG. 23	*C. pollex* Wagner & Ioff, 1926 U.S.S.R.—*Citellus*
FIG. 24.	*C. bisoctodentatus* Kolenati, 1863 Palaearctic—Talpids
FIG. 25.	*C. cryptotis* Traub & Barrera, 1966 Mexico—Shrews
FIG. 26.	*C. haagi* Traub, 1950 Mexico—Voles
FIG. 27.	*C. rettigi* Rothschild, 1908 U.S.S.R.—Cricetines
FIG. 28.	*C. l. levanticus* Lewis, 1964 Middle East—*Spalax*

VARIATIONS IN PRONOTAL COMBS — CTENOPHTHALMUS (I. 3)



21 C. EXPANSUS MYODOSUS TRAUB & BARRERA, 1966 MEXICO - SHREWS

22 C. A. AGYRTES (HELLER, 1896) PALAEARCTIC-VOLES, ETC.

23 C. POLLEX WAGNER & IOFF, 1926 U.S.S.R. -CITELLUS

24 C. BISOCTODENTATUS KOLENATI, 1863 PALAEARCTIC - TALPIDS

25 C. CRYPTOTIS TRAUB & BARRERA, 1966 MEXICO - SHREWS

26 C. HAAGI TRAUB, 1950 MEXICO - VOLES

27 C. RETTIGI ROTHSCHILD, 1908 U.S.S.R. -CRICETINES

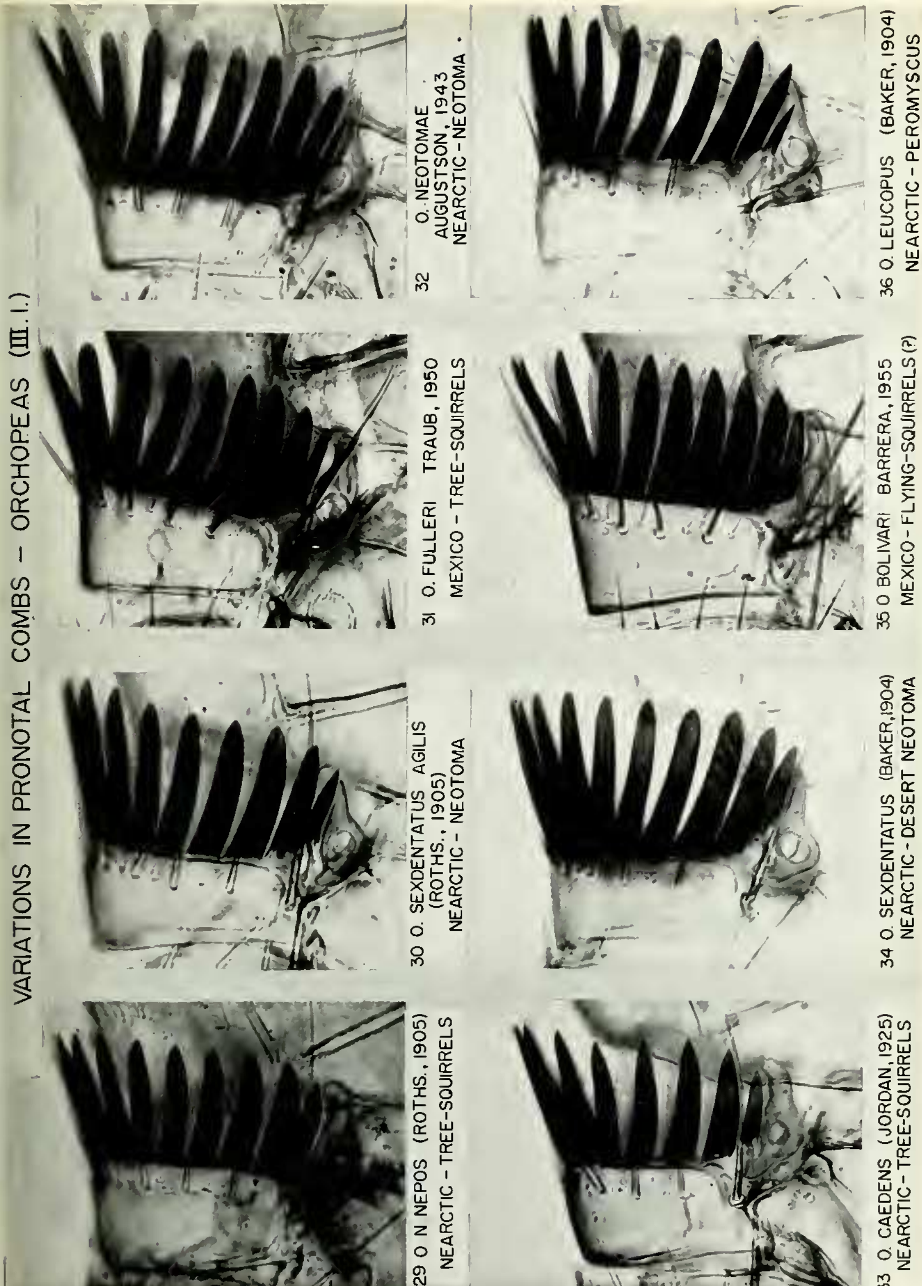
28 C. L. LEVANTICUS LEWIS, 1964 MIDDLE EAST - SPALAX

PLATE 5

Variations in Pronotal Combs— **Orchopeas** (iii.1)

FIG. 29	*O n. nepos* (Roths., 1905) Nearctic—Tree-Sqnirrels
FIG. 30.	*O. sexdentatus agilis* (Roths., 1905) Nearctic—*Neotoma*
FIG. 31.	*O. fulleri* Traub, 1950 Mexico—Tree-Squirrels
FIG. 32.	*O. neotomae* Augustson, 1943 Nearctic—*Neotoma*
FIG. 33	*O. caedens* (Jordan, 1925) Nearctic—Tree-squirrels
FIG. 34.	*O. sexdentatus* (Baker, 1904) Nearctic—Desert *Neotoma*
FIG. 35.	*O. bolivari* Barrera, 1955 Mexico—Flying-Squirrels (?)
FIG. 36.	*O. leucopus* (Baker, 1904) Nearctic—*Peromyscus*

VARIATIONS IN PRONOTAL COMBS – ORCHOPEAS (III.I.)



29 O N NEPOS (ROTHS., 1905) NEARCTIC - TREE-SQUIRRELS

30 O. SEXDENTATUS AGILIS (ROTHS., 1905) NEARCTIC - NEOTOMA

31 O. FULLERI TRAUB, 1950 MEXICO - TREE-SQUIRRELS

32 O. NEOTOMAE AUGUSTSON, 1943 NEARCTIC - NEOTOMA

33 O. CAEDENS (JORDAN, 1925) NEARCTIC - TREE-SQUIRRELS

34 O. SEXDENTATUS (BAKER, 1904) NEARCTIC - DESERT NEOTOMA

35 O BOLIVARI BARRERA, 1955 MEXICO - FLYING-SQUIRRELS (?)

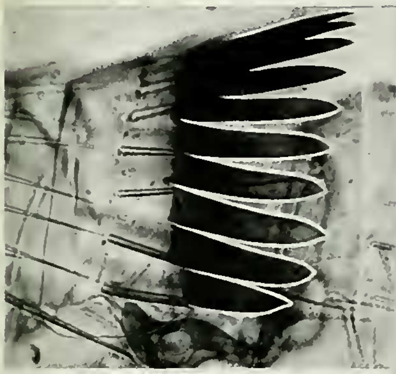
36 O. LEUCOPUS (BAKER, 1904) NEARCTIC - PEROMYSCUS

PLATE 6

Pronotal Combs—Sciurid Fleas Versus Murine Fleas in Genus **Neopsylla**

Fig. 37. (i.7) *Neopsylla setosa* (Wagner, 1898) Palaearctic—Chipmunk
Fig. 38. (i.7) *Neopsylla luma* Traub, 1954 Borneo—*Rattus*
Fig. 39. (i.7) *Neopsylla inopina* Roths., 1915 Nearctic—Ground-Squirrels
Fig. 40. (i.7) *Neopsylla dispar* Jordan, 1932 Malaysian—*Rattus*
Fig. 41 (i.7) *Neopsylla bidentatiformis* (Wagner, 1893) Palaearctic—Cricetines & Ground-Squirrels
Fig. 42 (i.7) *Neopsylla hissarica* Ioff & Sosnina, 1950 Palaearctic—*Rattus*

PRONOTAL COMBS – SCIURID FLEAS VERSUS MURINE FLEAS IN GENUS NEOPSYLLA



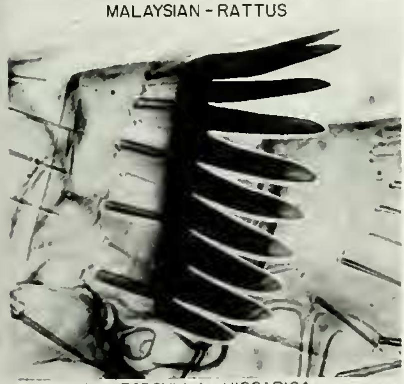
37 (I 7) NEOPSYLLA SETOSA (WAGNER, 1898) PALAEARCTIC – CHIPMUNK

38 (I.7) NEOPSYLLA LUMA TRAUB, 1954 BORNEO – RATTUS

39 (I 7) NEOPSYLLA INOPINA ROTHS., 1915 NEARCTIC – GROUND-SQUIRRELS

40 (I 7) NEOPSYLLA DISPAR JORDAN, 1932 MALAYSIAN – RATTUS

41 (I.7) NEOPSYLLA BIDENTATIFORMIS (WAGNER, 1893) PALAEARCTIC – CRICETINES & GROUND–SQUIRRELS



42 (I.7) NEOPSYLLA HISSARICA IOFF & SOSNINA, 1950 PALAEARCTIC – RATTUS

LIST OF ILLUSTRATIONS

PLATE 7

Pronotal Combs—**Opisodasys** (Nearctic)

PRONOTAL COMBS – OPISODASYS (NEARCTIC)

43 (III.1) OPISODASYS KEENI (BAKER, 1896)
PEROMYSCUS

44 (III.1) OPISODASYS HOLLANDI TRAUB, 1947
TREE – SQUIRREL

45 (III.1) OPISOOASYS NESIOTUS AUGUSTSON, 1941
PEROMYSCUS

46 (III.1) OPISODASYS ROBUSTUS (JORDAN, 1925)
TREE – SQUIRREL

47 (III.1) OPISODASYS PSEUDARCTOMYS (BAKER, 1904)
FLYING – SQUIRREL

48 (III.1) OPISODASYS ENOPLUS (ROTHS., 1909)
TREE – SQUIRREL

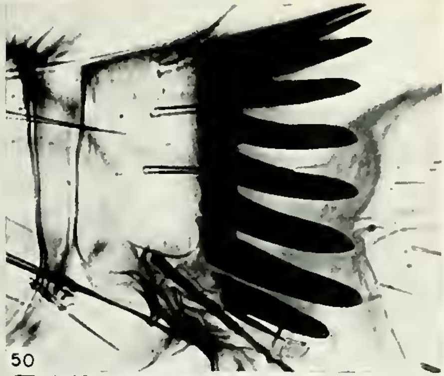
PLATE 8

Pronotal Combs—Fleas of Murines

FIG. 49. (iii.1) *Nosopsyllus londiniensis* (Roths., 1903) Egypt (and introduced)—*Arvicanthis* and Rats
FIG. 50. (iv.2) *Acropsylla girshami* Traub, 1950 Eastern Palaearctic—*Mus*
FIG. 51 (ii.1) *Stivalius* (*Gryphopsylla*) *hopkinsi* Traub, 1957 Borneo—*Rattus*
FIG. 52. (ii.1) *Stivalius cognatus spiramus* Jordan, 1926 Philippines—*Rattus* (*Rattus*)
FIG. 53. (iv.1) *Leptopsylla pamirensis* (Ioff, 1946) Eastern Palaearctic—*Apodemus*
FIG. 54 (iv.1) *Sigmactenus alticola* Traub, 1954 Borneo—*Rattus* (*Rattus*)

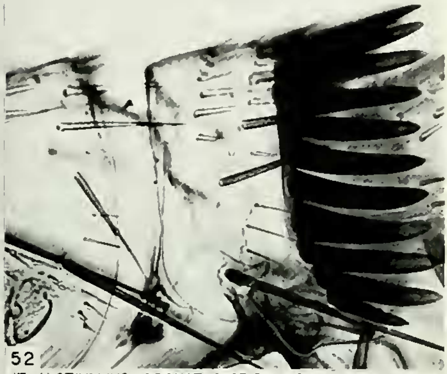
PRONOTAL COMBS – FLEAS OF MURINES

49
(III 1) NOSOPSYLLUS LONDINIENSIS (ROTHSCHILD, 1903)
EGYPT (AND INTRODUCED) – ARVICANTIS & RATS



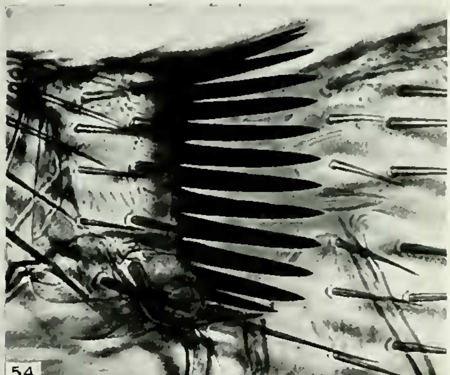
50
(IV. 2) ACROPSYLLA GIRSHAMI TRAUB, 1950
EASTERN PALAEARCTIC – MUS

51
(II. 1) STIVALIUS (GRYPHOPSYLLA) HOPKINSI TRAUB, 1957
BORNEO – RATTUS



52
(II. 1) STIVALIUS COGNATUS SPIRAMUS JORDAN, 1926
PHILIPPINES – RATTUS (RATTUS)

53
(IV. 1) LEPTOPSYLLA PAMIRENSIS (IOFF, 1946)
EASTERN PALAEARCTIC – APODEMUS



54
(IV. 1) SIGMACTENUS ALTICOLA TRAUB, 1954
BORNEO – RATTUS (RATTUS)

PLATE 9

Pronotal Combs—**Monopsyllus** (iii.1)

FIG. 55. *Monopsyllus exilis* (Jordan, 1937) ex *Onychomys*—U.S.A

FIG. 56. *Monopsyllus indages* (Rothschild, 1908) ex Squirrels and Chipmunks—Palaearctic

FIG. 57. *Monopsyllus thambus* (Jordan, 1929) ex *Peromyscus*—Nearctic (North)

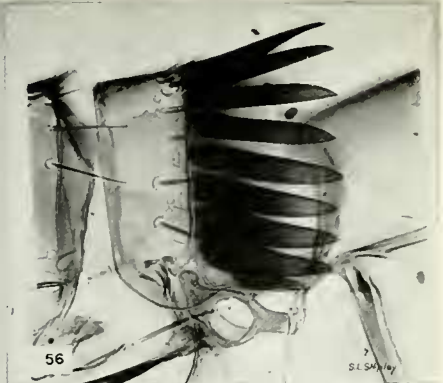
FIG. 58. *Monopsyllus argus* (Rothschild, 1908) ex Flying-Squirrel—Palaearctic

FIG. 59. *Monopsyllus wagneri* (Baker, 1904) ex *Peromyscus*, etc.—North America

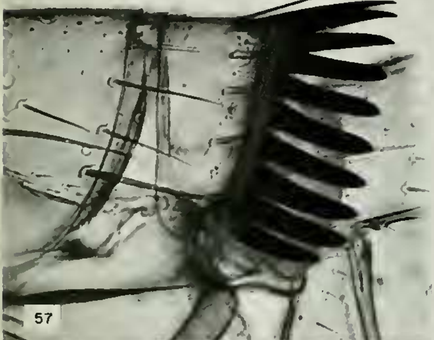
FIG. 60. *Monopsyllus sciurorum* (Schrank, 1803) ex Dormice—Palaearctic

PRONOTAL COMBS — MONOPSYLLUS (III.1)

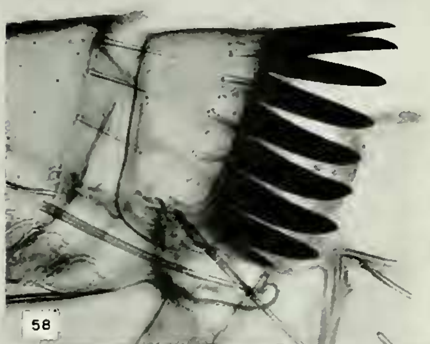
MONOPSYLLUS EXILIS (JORDAN, 1937)
EX. ONYCHOMYS - U.S.A.



MONOPSYLLUS INDAGES (ROTHSCHILD, 1908)
EX. SQUIRRELS & CHIPMUNKS - PALAEARCTIC



MONOPSYLLUS THAMBUS (JORDAN, 1929)
EX. PEROMYSCUS - NEARCTIC (NORTH)



MONOPSYLLUS ARGUS (ROTHSCHILD, 1908)
EX FLYING-SQUIRREL-PALAEARCTIC

MONOPSYLLUS WAGNERI (BAKER, 1904)
EX. PEROMYSCUS, ETC.-NORTH AMERICA

MONOPSYLLUS SCIURORUM (SCHRANK, 1803)
EX. DORMICE - PALAEARCTIC

PLATE 10

Pronotal Combs **Monopsyllus** (iii.1)

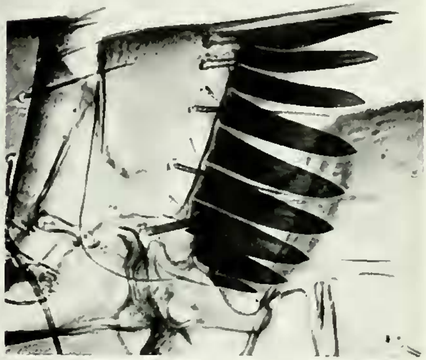
Fig. 61	*Monopsyllus anisus* (Rothschild, 1907) Murids, etc.—Palaearctic
Fig. 62.	*Monopsyllus ciliatus protinus* (Jordan, 1929) *Tamiasciurus, Eutamias* Nearctic
Fig. 63	*Monopsyllus tolli* (Wagner, 1901) *Ochotona*—Holarctic
Fig. 64.	*Monopsyllus vison* (Baker, 1904) *Tamiasciurus*—Nearctic
Fig. 65.	*Monopsyllus eutamiadis* Augustson, 1941 Chipmunks—California
Fig. 66.	*Monopsyllus fornacis* Jordan, 1937 Chipmunks—California

PRONOTAL COMBS–MONOPSYLLUS (III.1)

61 MONOPSYLLUS ANISUS (ROTHSCHILD, 1907)
PALAEARCTIC–MURIDS, ETC.

62 MONOPSYLLUS CILIATUS PROTINUS (JORDAN, 1929)
NEARCTIC–TAMIASCIURUS, EUTAMIAS

63 MONOPSYLLUS TOLLI (WAGNER, 1901)
HOLARCTIC–OCHOTONA



64 MONOPSYLLUS VISON (BAKER, 1904)
NEARCTIC–TAMIASCIURUS

65 MONOPSYLLUS EUTAMIADIS AUGUSTSON, 1941
CALIFORNIA–CHIPMUNKS

66 MONOPSYLLUS FORNACIS JORDAN, 1937
CALIFORNIA–CHIPMUNKS

PLATE 11

Pronotal Combs—Fleas of Underground Nests

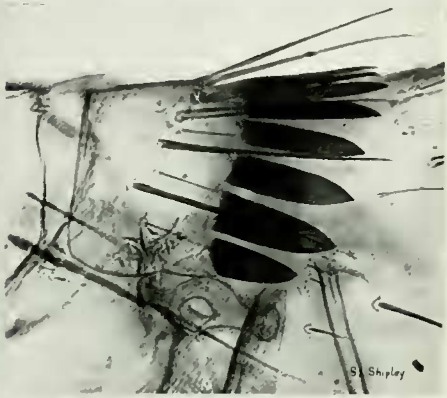
FIG. 67. (i.7) *Catallagia charlottensis* (Baker, 1898) N. America—*Peromyscus*, etc.
FIG. 68. (iii.1) *Pleochaetis paramundus* Traub, 1950 Mexico—*Neotomodon*
FIG. 69. (i.7) *Epitedia cavernicola* Traub, 1957 U.S.A.—*Neotoma*
FIG. 70. (i.7) *Genoneopsylla thysanota* (Traub, 1968) Nepal—*Ochotona*
FIG. 71 (iv.2) *Caenopsylla laptevi* Mikulin & Zagniborodova, 1958 S.W. Asia (Hosts?)
FIG. 72. (i.8) *Rhadinopsylla mexicana* (Barrera, 1952) Mexico—Peromyscines

PRONOTAL COMBS- FLEAS OF UNDERGROUND NESTS

67 (I 7) CATALLAGIA CHARLOTTENSIS (BAKER, 1898)
N AMERICA–PEROMYSCUS, ETC.

68 (III 1) PLEOCHAETIS PARAMUNDUS TRAUB, 1950
MEXICO – NEOTOMODON

69 (I 7) EPITEDIA CAVERNICOLA TRAUB, 1957
U S A — NEOTOMA



70 (I 7) GENONEOPSYLLA THYSANOTA (TRAUB, 1968)
NEPAL — OCHOTONA

71 (IV. 2) CAENOPSYLLA LAPTEVI MIKULIN & ZAGNIBORODOVA, 1958 SW ASIA–(HOST?)

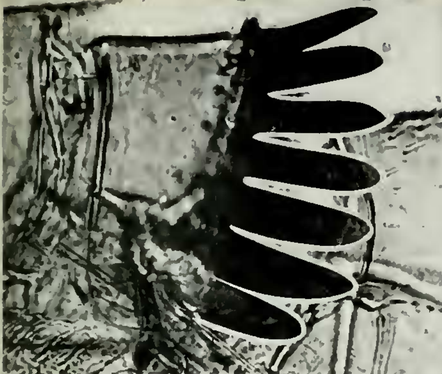
72 (I.8) RHADINOPSYLLA MEXICANA (BARRERA, 1952)
MEXICO-PEROMYSCINES

PLATE 12

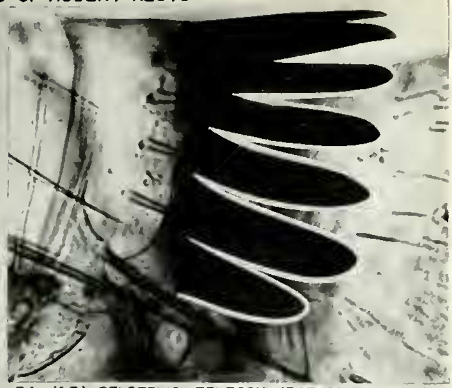
Pronotal Combs—Fleas of Rodent Nests

FIG. 73. (1.2) *Conorhinopsylla stanfordi* Stewart, 1930 Eastern U.S.A.—Squirrels
FIG. 74. (1.7) *Delotelis telegoni* (Rothschild, 1905) Western No. America—*Peromyscus*
FIG. 75. (1.2) *Megarthroglossus procus* J. & R., 1915 Western No. America—Squirrels
FIG. 76. (1.7) *Tamiophila grandis* (Rothschild, 1902) Eastern No. America—Chipmunks
FIG. 77. (1.7) *Epitedia faceta* (Rothschild, 1915) Eastern U.S.A.—Squirrels
FIG. 78. (1.7) *Phalacropsylla paradisea* Roths., 1915 So. Western U.S.—*Neotoma*

PRONOTAL COMBS — FLEAS OF RODENT NESTS



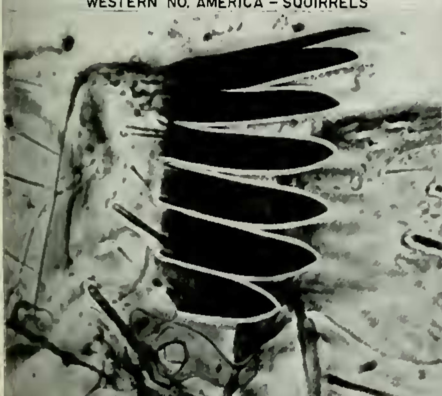
73 (I 2) CONORHINOPSYLLA STANFORDI STEWART, 1930
EASTERN U.S.A.–SQUIRRELS



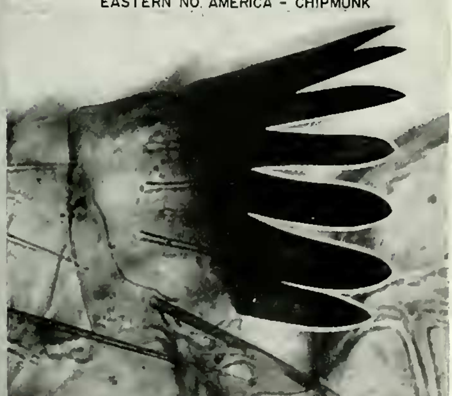
74 (I.7) DELOTELIS TELEGONI (ROTHSCHILD, 1905)
WESTERN NO AMERICA – PEROMYSCUS

75 (I. 2) MEGARTHROGLOSSUS PROCUS J. & R., 1915
WESTERN NO. AMERICA – SQUIRRELS

76 (I 7) TAMIOPHILA GRANDIS (ROTHSCHILD, 1902)
EASTERN NO. AMERICA – CHIPMUNK



77 (I.7) EPITEDIA FACETA (ROTHSCHILD, 1915)
EASTERN U.S.A.–SQUIRRELS



78 (I.7) PHALACROPSYLLA PARADISEA ROTHS., 1915
SO. WESTERN U.S. – NEOTOMA

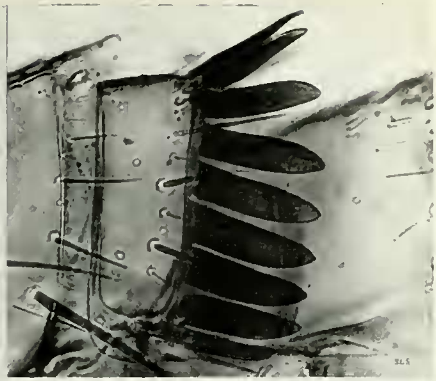
PLATE 13

Pronotal Combs—Fleas of Underground Nests

FIG. 79. (i.7) *Strepsylla mina* Traub, 1950 Mexico—*Neotomodon*
FIG. 80. (iv.2) *Phaenopsylla kopetdag* Ioff, 1946 S.W. Asia—*Calomyscus*
FIG. 81. (i.7) *Catallagia striata* Scalon, 1950 E. Palaearctic Voles
FIG. 82. (iv.2) *Paradoxopsyllus microphthalmus* Ioff, 1946 S.W. Asia *Calomyscus*
FIG. 83. (i.2) *Wagnerina schelkovnikovi* Ioff & Argyropulo, 1934 S.W. Asia—*Meriones*
FIG. 84. (iii.1) *Callopsylla dolabris* (J. & R., 1911) S.E. Palaearctic—*Marmota*

PRONOTAL COMBS—FLEAS OF UNDERGROUND NESTS

79 (I.7) STREPSYLLA MINA TRAUB, 1950
MEXICO—NEOTOMODON



80 (IV 2) PHAENOPSYLLA KOPETDAG IOFF, 1946
SOUTH WESTERN ASIA—CALOMYSCUS

81 (I.7) CATALLAGIA STRIATA SCALON, 1950
EAST PALAEARCTIC—VOLES

82 (IV 2) PARADOXOPSYLLUS MICROPHTHALMUS IOFF, 1946
SOUTH WESTERN ASIA—CALOMYSCUS

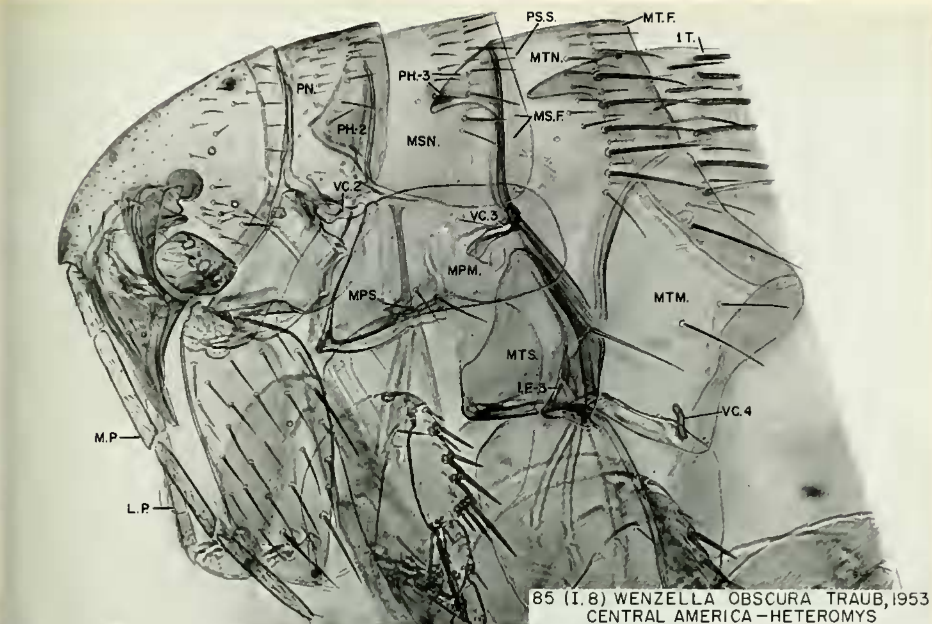
83 (I.2) WAGNERINA SCHELKOVNIKOVI IOFF & ARGYROPULO, 1934
SOUTH WESTERN ASIA—MERIONES

84 (III.1) CALLOPSYLLA DOLABRIS (J & R., 1911)
SOUTH EASTERN PALAEARCTIC—MARMOTA

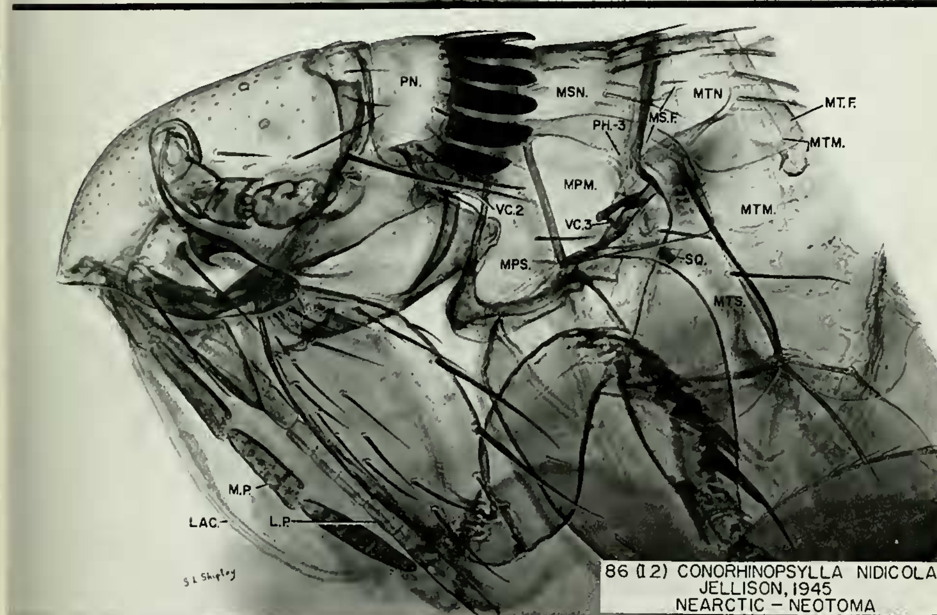
PLATE 14

Head and Thorax of Some Nest-Fleas

FIG. 85 (1.8) *Wenzella obscura* Traub, 1953 Central America—*Heteromys*
FIG. 86. (1.2) *Conorhinopsylla nidicola* Jellison, 1945 Nearctic—*Neotoma*



85 (I. 8) WENZELLA OBSCURA TRAUB, 1953
CENTRAL AMERICA–HETEROMYS



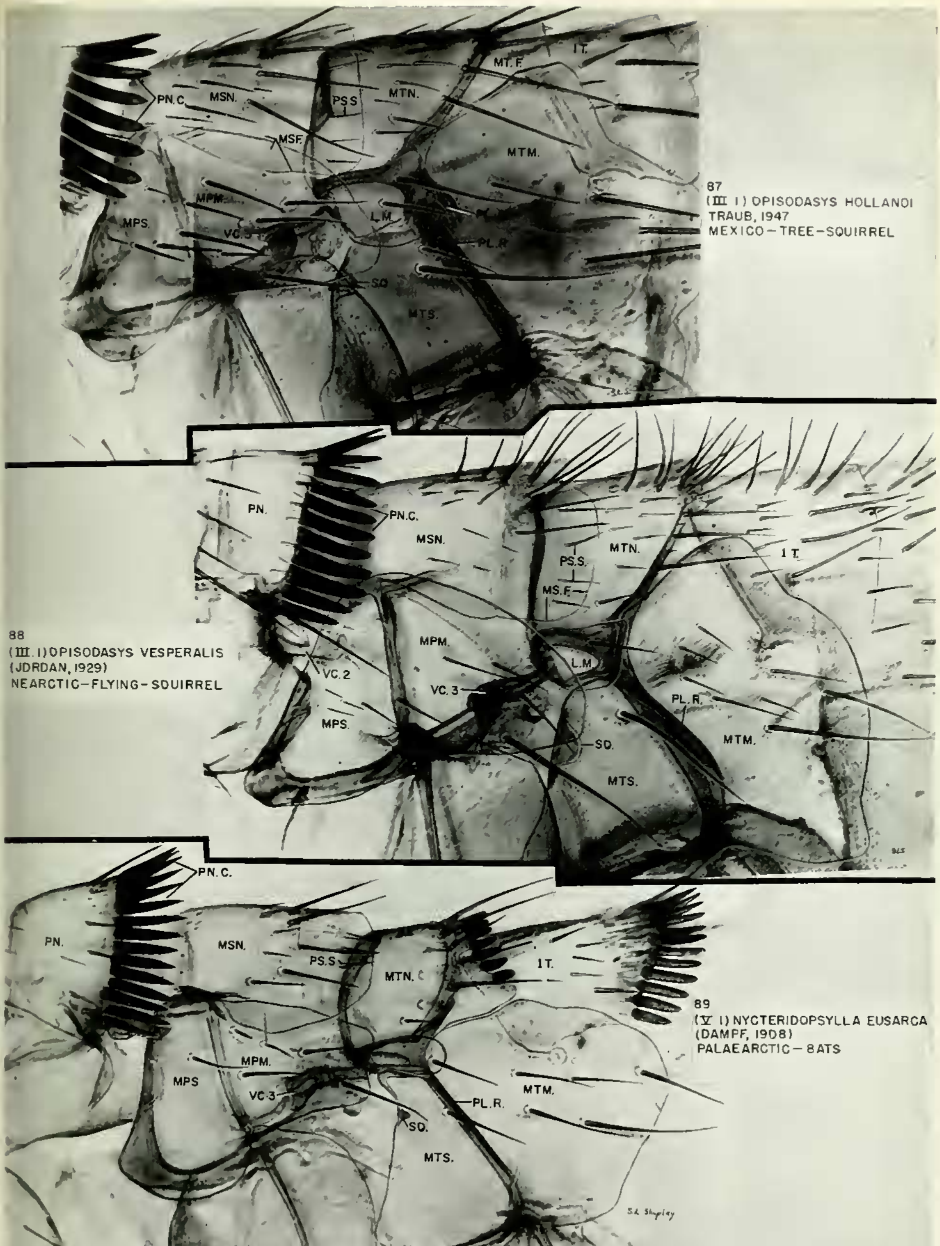
86 (I. 2) CONORHINOPSYLLA NIDICOLA
JELLISON, 1945
NEARCTIC – NEOTOMA

HEAD AND THORAX OF SOME NEST-FLEAS

PLATE 15

Some Examples of the Thorax of Fleas

FIG. 87. (iii.1) *Opisodasys hollandi* Traub, 1947 Mexico Tree-Squirrels
FIG. 88. (iii.1) *Opisodasys vesperalis* (Jordan, 1929) Nearctic—Flying-Squirrel
FIG. 89 (v.1) *Nycteridopsylla eusarca* (Dampf, 1908) Palaearctic—Bats



87
(III 1) OPISODASYS HOLLANDI TRAUB, 1947
MEXICO–TREE–SQUIRREL

88
(III. 1) OPISODASYS VESPERALIS (JORDAN, 1929)
NEARCTIC–FLYING–SQUIRREL

89
(V 1) NYCTERIDOPSYLLA EUSARCA (DAMPF, 1908)
PALAEARCTIC–BATS

SOME EXAMPLES OF THE THORAX OF FLEAS

PLATE 16

Head and Thorax of Two **Ceratophyllus** From Cliff-Swallows

FIG. 90. (iii.1) *Ceratophyllus arcuegens* Holland, 1952 Palaearctic
FIG. 91. (iii.1) *Ceratophyllus styx* Rothschild, 1900 Palaearctic

90 (III. 1) CERATOPHYLLUS ARCUEGENS HOLLAND, 1952
NEARCTIC

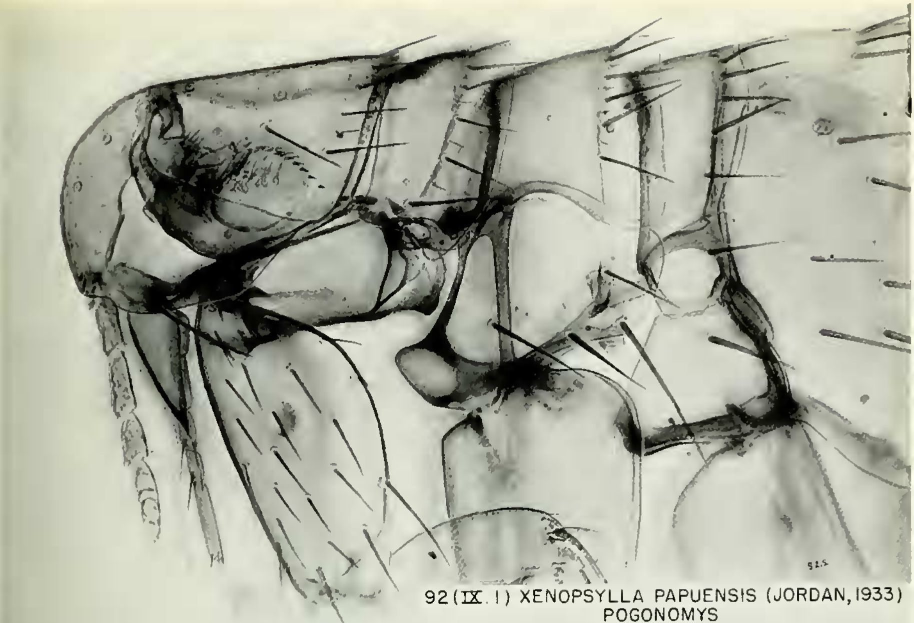
91 (III. 1) CERATOPHYLLUS STYX ROTHSCHILD, 1900
PALAEARCTIC

HEAD AND THORAX OF TWO CERATOPHYLLUS FROM CLIFF-SWALLOWS

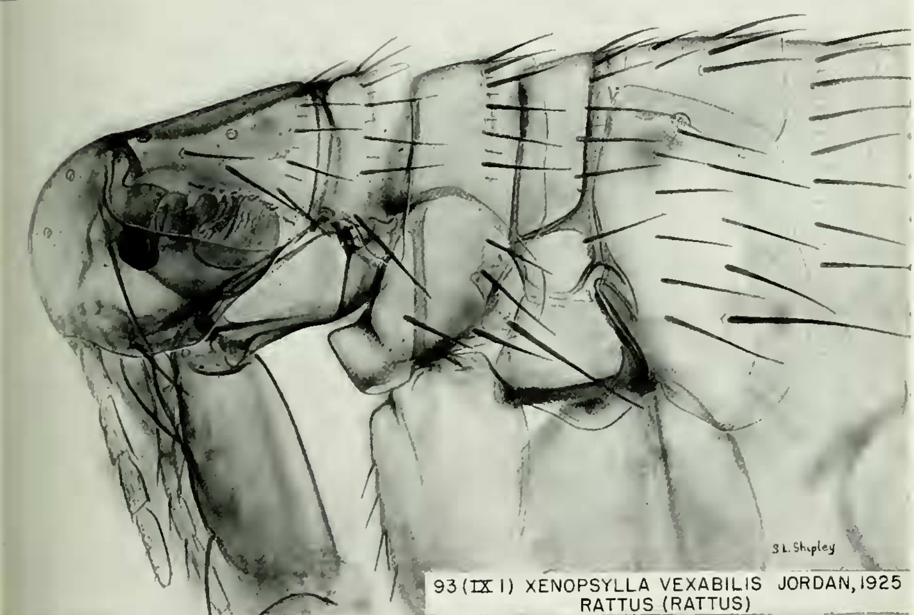
PLATE 17

Head and Thorax of Two **Xenopsylla** from New Guinea

FIG. 92. (ix 1) *Xenopsylla papuensis* (Jordan, 1933) *Pogonomys*
FIG. 93. (ix 1) *Xenopsylla vexabilis* Jordan, 1925 *Rattus* (*Rattus*)



92 (IX. 1) XENOPSYLLA PAPUENSIS (JORDAN, 1933)
POGONOMYS



93 (IX 1) XENOPSYLLA VEXABILIS JORDAN, 1925
RATTUS (RATTUS)

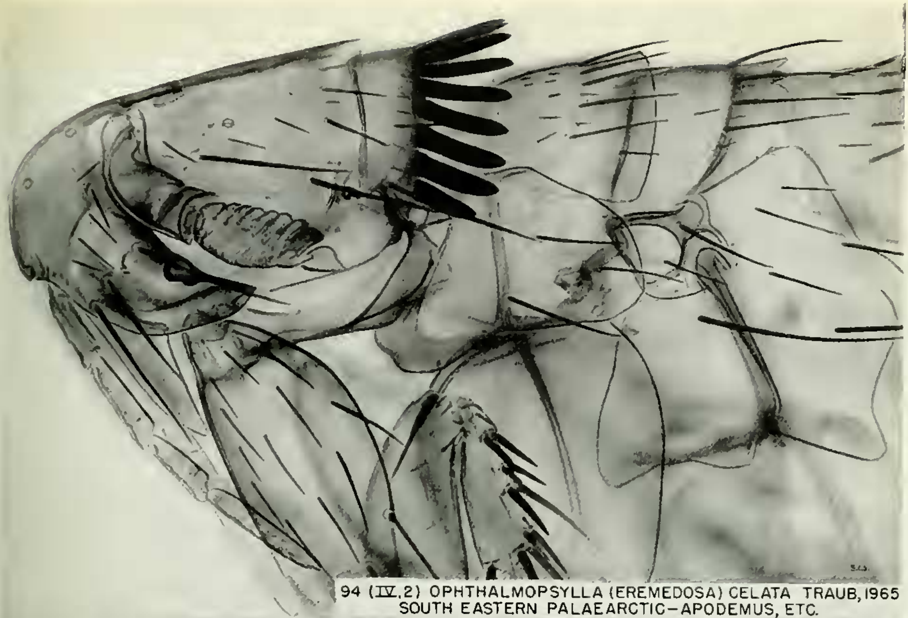
HEAD AND THORAX OF TWO XENOPSYLLA FROM NEW GUINEA

PLATE 18

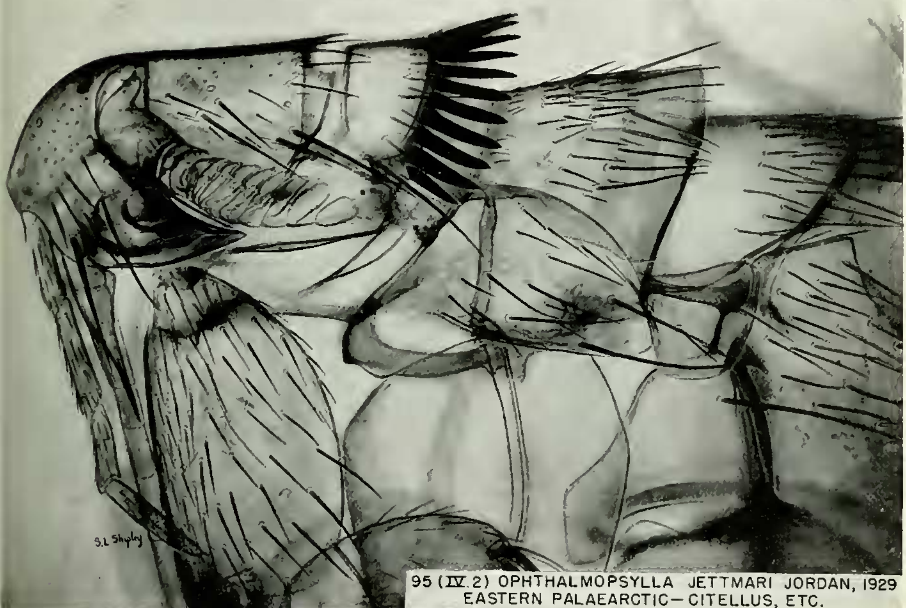
Head and Thorax of Two **Ophthalmopsylla**

FIG. 94. (iv.2) *Ophthalmopsylla* (*Eremedosa*) *celata* Traub, 1965 S.E. Palaearctic—*Apodemus*, etc.

FIG. 95. (iv.2) *Ophthalmopsylla jettmari* Jordan, 1929 E. Palaearctic—*Citellus*, etc.



94 (IV.2) OPHTHALMOPSYLLA (EREMEDOSA) CELATA TRAUB, 1965
SOUTH EASTERN PALAEARCTIC—APODEMUS, ETC.



95 (IV.2) OPHTHALMOPSYLLA JETTMARI JORDAN, 1929
EASTERN PALAEARCTIC—CITELLUS, ETC.

HEAD AND THORAX OF TWO OPHTHALMOPSYLLA

PLATE 19

Contrasts in Head and Prothorax of Some Fleas

FIG. 96. (iii.1) *Macrostylophora borneensis* (Jordan, 1926) Borneo—Ground-Squirrels
FIG. 97. (iii.1) *Macrostylophora fimbriata* (J. & R., 1921) Himalayan—Flying-Squirrels
FIG. 98. (i.7) *Epitedia stanfordi* Traub, 1944 S.W. U.S.A. *Peromyscus*
FIG. 99. (ix 1) *Actenopsyllus suavis* J. & R., 1923 California—Sea-Birds

CONTRASTS IN HEAD AND PROTHORAX OF SOME FLEAS

96 (III 1) MACROSTYLOPHORA BORNEENSIS (JORDAN, 1926)
BORNEO–GROUND–SQUIRRELS

97 (III 1) MACROSTYLOPHORA FIMBRIATA (J. & R., 1921)
HIMALAYAN–FLYING–SQUIRRELS

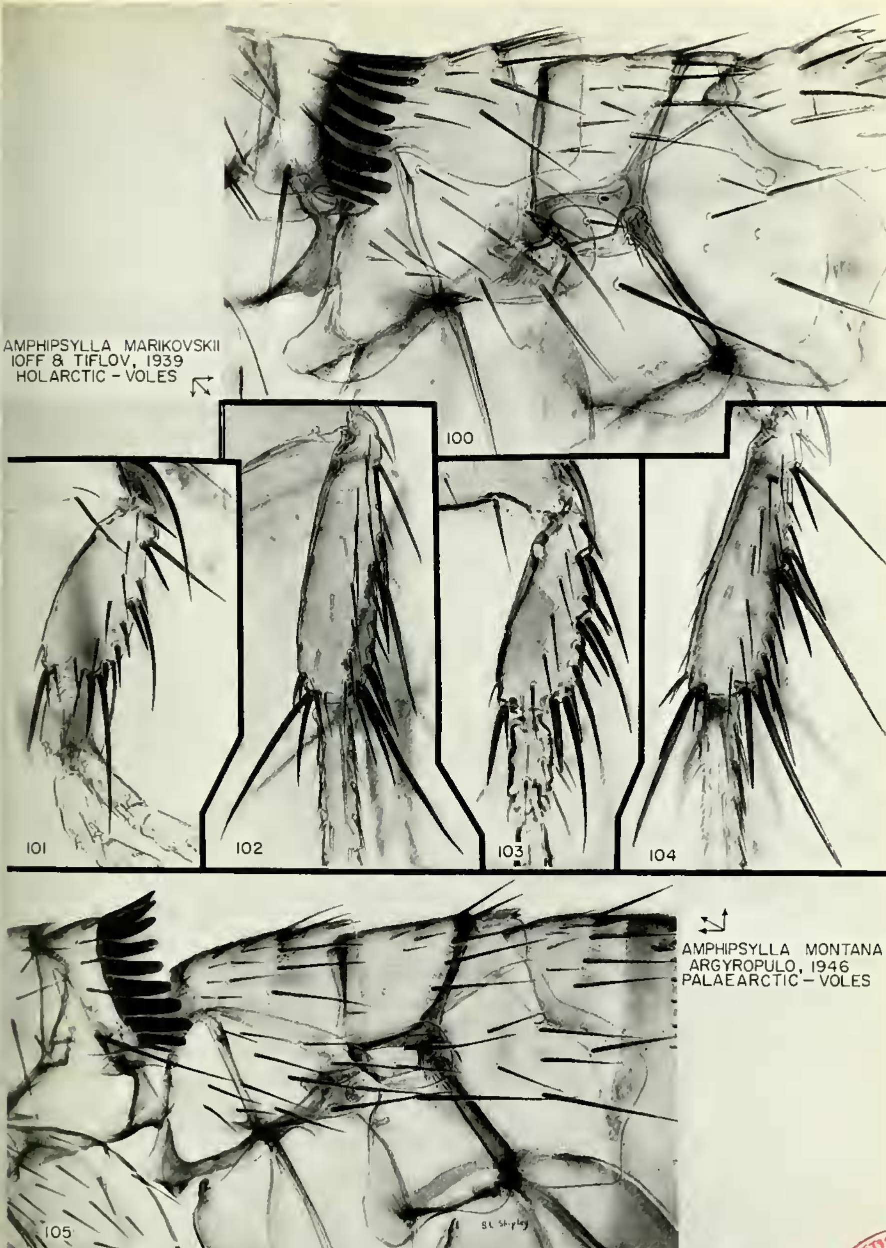
98 (I.7) EPITEDIA STANFORDI TRAUB, 1944
SOUTH WESTERN U.S.A.–PEROMYSCUS

99 (IX. 1) ACTENOPSYLLUS SUAVIS J. & R., 1923
CALIFORNIA–SEA-BIRDS

PLATE 20

Thorax, Pro- and Metatibia of Two **Amphipsylla** (iv.2)

FIG. 100.	*Amphipsylla marikovskii* Ioff & Tiflov, 1939	Holarctic—Voles
FIG. 101.	*Amphipsylla marikovskii* Ioff & Tiflov, 1939	Holarctic—Voles
FIG. 102.	*Amphipsylla marikovskii* Ioff & Tiflov, 1939	Holarctic—Voles
FIG. 103.	*Amphipsylla montana* Argyropulo, 1946	Palaearctic—Voles
FIG. 104	*Amphipsylla montana* Argyropulo, 1946	Palaearctic—Voles
FIG. 105.	*Amphipsylla montana* Argyropulo, 1946	Palaearctic—Voles



THORAX, PRO- & METATIBIA OF TWO AMPHIPSYLLA (IV. 2)